STROMATOPOROID PALAEOECOLOGY AND SYSTEMATICS FROM THE MIDDLE DEVONIAN FANNING RIVER GROUP, NORTH QUEENSLAND

ALEX G. COOK

Thirty five stromatoporoid taxa are described from the Middle Devonian (Givetian) lower Fanning River Group, Burdekin Subprovince, north Queensland, Australia.

Ten faunal communities are recognised, based on the study and distribution of stromatoporoid and selected molluscan taxa, and the distribution of tabulate and rugose corals. The *Burdikinia* community, characterised by robust gastropods, occupied the coarse siliciclastic inner shelf. The *Modiomorpha* community is represented by a near-shore, in situ shell bed. The *Stachyodes costulata-Syringopora* community lived in inner shelf muddy carbonate-dominated lagoons, but was in part able to inhabit subtidal interstitial niches of marine headlands. In the Fletcherview-Burdekin Downs area, the *Hermatostroma maculatum-Gerronostroma hendersoni* community constructed lagoonal patch reefs, back-reef laminar stromatoporoid pavements and bioherms. The *Clathrocoilona spissa-Aulopora* community occupied nearshore, fringing biostromes in the Fanning River area. *Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus* community occupied extensive nearshore to offshore biostromes within the Fanning River-Golden Valley areas. The *Coenostroma-Hermatostroma episcopale* community dwelt within dispersed stromatoporoid pavements and less commonly, within offshore coralline thickets. The *Amphipora pervesiculata* community characterised by dendroid stromatoporoid-coralline thickets adjacent to and seaward of bioherms, dispersed stromatoporoid pavements and stromatoporoid biostromes, particularly in the Fletcherview-Burdekin Downs area. The *Endophyllum* community was restricted to patch reefs which grew during a regressive phase, carbonate to siliciclastic transition. A cephalopod association is represented by a sparse fauna occurring within deeper water micritic facies in the Golden Valley area.

Analysis of stromatoporoid shape demonstrates the influence of both genetic and ecologic factors. Zonation of skeletal shape, apparent for both biostromal and biohermal complexes, indicates that strong ecologic influences dominated. Substrate type, sedimentation rate and water depth were important controls. Most taxa display a range of shape. Complex overgrowth phenomena, between stromatoporoid taxa, tabulate corals, chaetetids and algae produced compound skeletons that are most common within nearshore biostromes, and are interpreted to indicate stress imposed by repeated lethal depositional events or by seasonal variations in salinity.

Intergrowths of stromatoporoids with tabulate corals *Syringoporella?* sp. and *Syringopora* sp., a number of rugose corals and a ?vermetid are documented. *Syringoporella?* sp. is more common in stromatoporoids with irregular skeletal architecture. For *Syringoporella?* sp. an even distribution of corallites within the host, skeletal response to corallite occurrence and the absence of micritic envelopes suggests a symbiotic relationship with both the coral and the stromatoporoid accreting at the same rate and maintaining an even growth surface.

Six new species of stromatoporoids are described comprising *Gerronostroma hendersoni*, *Trupetostroma zheni*, *Euryamphipora merlini*, *Ferestromatopora heideckeri*, *Coenostroma burdekinense* and *Coenostroma wyatti*.

Biogeographic affinities of the fauna are strongly with the Old World Realm, with species level affinities with Guangxi, Poland and Belgium. □ *Stromatoporoids, taxonomy, north Queensland, Middle Devonian, palaeoecology.*

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Stromatoporoids are major faunal elements of the ?Eifelian-Givetian Fanning River Group, which cropout extensively within the Burdekin Subprovince, Townsville hinterland, north Queensland. This study examines the ecology and systematics of the stromatoporoid faunas.
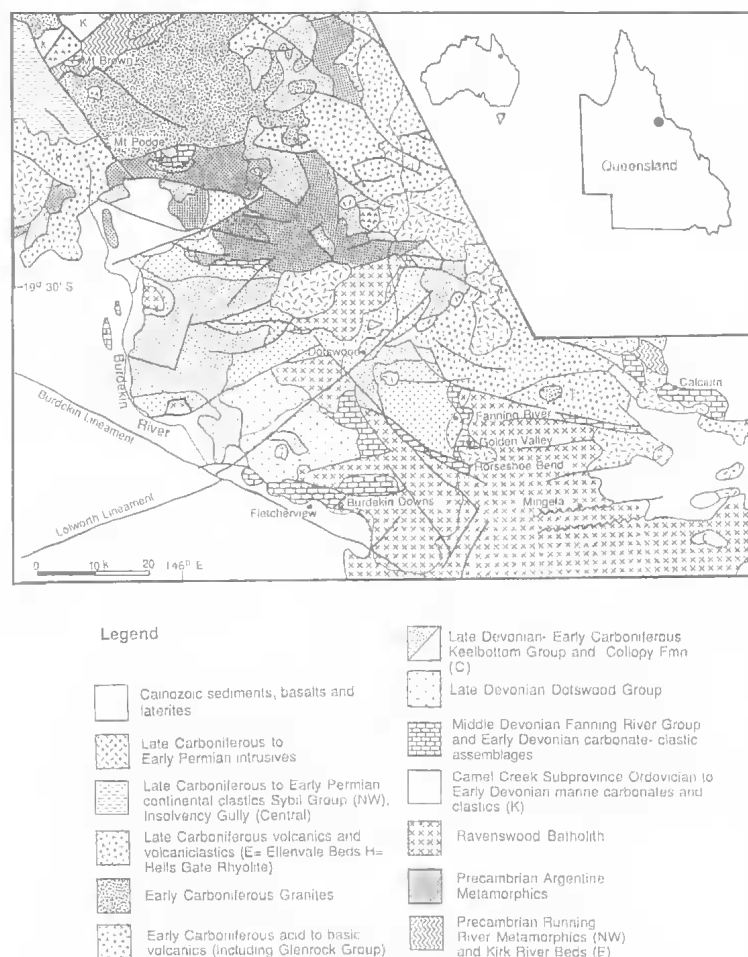
FIG. 1. Geological map of the Burdekin Subprovince after Lang et al. (1990).

plain coarse-grained fluvial ehannel and finer-grained floodplain deposits. Deposition within the inner shelf was complex refleeting local influences of coarse silieielastie input, inner shelf carbonate production and an across-shelf siliciclastie to carbonate transition. Faeies deposited in the inner shelf are: (1) abraded coarse silieielastie facies representing inundated marine headlands, and eoarse siliciclasties representing upper shoreface deposition, (2) fossiliferous sandstone facies deposited on the lower shorefaee to subtidal zone, (3) fossiliferous siltstone faeies, representing restrieted fine-grained siliciclastic-dominated, nearshore, subtidal embayments, (4) nodular limestone facies deposited within mostly subtidal, carbonate-dominated, impure lagoons with local patch reef development, (5) impure limestone-sandstone faeies representing sporadie depos-ition of mobile eoarse silieiclastie sand bodies within impure, subtidal carbonate lagoons. Deposition on the proximal shelf was dominated by stromatoporoid biostromal faeies (seven divisions) representing biohermal (reefal) deposition (framestone), baek-reef or intra-biostromal stromatoporoid pavement (eoverstone), interreef ehannel (grainy floatstone), and extensive biostromes and storm-reworked equivalents which developed from the nearshore zone aeross the shallow shelf (silty rubbly floatstone, mieritie stromatoporoid floatstone, rudstone, assoeiated packstone and wackestone). Reef and biostromal growth took place during moderate levels of siliciclastic input, in elose proximity to the granitie hinterland and ean be considered as preserved 'fringing' reef and biostrome. Additionally where extensive reef or biostrome did not develop, the proximal shelf was inhabited by dispersed stromatoporoid pavements (dispersed stromatoporoid paekstone facies). Three facies

The Fanning River Group is the lowermost stratigraphic unit of the Burdekin Subprovinee, a Middle Devonian to Carboniferous succession WSW of Townsville (Fig. 1). The Group consists of 3 formations; Big Bend Arkose, Burdekin Formation and Cultivation Gully Formation. In a recent sedimentologieal study (Cook, 1995), 12 distinet faeies have been identified from the Middle Devonian, ?Eifelian-Givetian Big Bend Arkose and Burdekin Formation, of the Fanning R. Group. They represent deposition within the restrieted Burdekin Basin in non-marine, inner and proximal shallow water marine shelf, and shallow to moderate depth, distal marine shelf environments. Non-marine deposition (unfossiliferous eoarse siliciclastie faeies) took plaee within restrieted eoastal plains, and represents in situ weathering profiles and coastal

represent distal shelf deposition, seaward of biohermal or biostromal growth: (1) coralline packstone, representing shallow water, offshore, coral and dendroid stromatoporoid thickets, (2) localised crinoid grainstone deposited as mobile carbonate sand bodies on the shallow distal shelf removed from significant siliciclastic input, (3) micritic carbonate facies, restricted to the Golden Valley area, representing relatively deeper water deposition at the limits of the photic zone. *Endophyllum* siltstone facies represents growth of small, coral-dominant patch reefs in a fine-grained mixed carbonate-siliciclastic environment during initial stages of regression in the uppermost Burdekin Formation within the Fanning R. area.

Deposition was controlled by basement topography and restricted basin geography with significant variations across the subprovince. For a review of the stratigraphy see Draper & Lang (1994), or Cook (1995).

Stromatoporoids are dominantly found within the Burdekin Formation, which based on the conodont studies of Talent & Mawson (1994) has been assigned a mostly Givetian age; see also Cook (1995).

Localities mentioned in this report are detailed in Cook (1995). Material is deposited at James Cook University of North Queensland, with a small collection at the Queensland Museum. Prefixes used in this work are JCUL for James Cook University geological locality and JCUF for James Cook University Fossil collection.

PREVIOUS PALAEONTOLOGICAL STUDIES

Palaeontological investigations of the Fanning River Group commenced with the work of Clarke (in Leichhardt 1847) who described '*Cyathophyllum leichhardti*' from the Burdekin River. Nicholson & Etheridge (1879), Etheridge (1880), Etheridge & Foord (1884), Jack & Etheridge (1892) and Etheridge (1917a, 1917b) all contain descriptions and lists of fossil collections from the Burdekin. Nicholson & Etheridge (1879) also described a number of tabulate corals from the Fanning R. and Arthurs Ck areas. They also briefly documented the presence of *Stromatopora* and *Caunopora* from Arthurs Ck, representing the first record of stromatoporoids from the Burdekin. Etheridge (1880) described 5 brachiopod taxa from the Fanning R. area collected by Robert Logan Jack.

Etheridge & Foord (1884) described 2 coral taxa and one chaetetid taxon from the Reid's Gap area.

Jack & Etheridge (1892) described and illustrated many faunal elements from the Burdekin Formation as part of the monograph on the Geology and Palaeontology of Queensland. Included were the first description and illustrations of stromatoporoids from the region with *Stromatopora* described and illustrated and *Stromatoporella* illustrated but not described. Etheridge (1917a) erected the gastropod species *Polyamma burdekinensis* subsequently revised by Knight (1937) and Heidecker (1959). Etheridge (1917b) described the polyzoan *Vetofistula miribalis* from the limestones at Reid's Gap, but this has subsequently been referred to as a species of the tabulate coral *Cladopora* (Hill 1981).

Hill (1942) made a detailed study of the rugose corals from 3 localities in the Burdekin Subprovince; Fanning R., Burdekin Downs and Reid's Gap. She illustrated and described 23 species of rugosans and mentioned the ramose stromatoporoid *Amphipora*, the brachiopods *Atrypa* and *Stringocephalus*, and the gastropod *Polyamma*. She also assigned a mid-Givetian age to the beds based on their similarities to European faunas. Brown (1944) briefly described *Stringocephalus burtini* Defrance from Fanning R. and Reid's Gap, also attributing a Givetian age to the limestone units. Heidecker (1959) described 4 molluscan genera (1 bivalve and 3 gastropods) of which 3 were new, from the Big Bend Arkose and Burdekin Formation near Lowes Basin. In Hill, Woods & Playford (1967) an unnamed stromatoporoid and a number of molluscan, rugose coral and tabulate coral taxa from the Burdekin Formation were illustrated. Strusz (1969) and Strusz & Jell (1971) discussed rugose coral taxa from the Fanning R. Group. West (1974) recognised 3 informal biostratigraphic zones as part of a study of the rugose corals at Fanning R. : the *Temnophyllum* sp. nov. range zone, the *Stringophyllum* sp. cf. *quasinormale* assemblage, and the *Endophyllum abditum columna* range zone. West (1974) inferred an early- to mid-Givetian age for the sequence but qualified the utility of these zones with a discussion of the facies dependence of the coralline forms. In addition, West (1974) mentioned and illustrated a number of tabulate corals and *Amphipora* spp. Stephenson (1977) documented a number of rugose and tabulate corals from the Fletcherview area. Henderson (1984) discussed the diagenetic origin of silica

within a 'Hermatoporoidea' type stromatoporoid from Fanning R. A major study of the rugose coral fauna was undertaken by Zhen (1991) who identified 10 coral assemblages within the Fanning R. Group *sensu lato*, comprised of 79 species and subspecies distributed amongst 41 genera of rugose coral. Zhen (1991) provided the basis for rugose coral identifications given in the present work. He briefly noted the presence of some stromatoporoid taxa, but did not attempt their systematic evaluation. Jell et al. (1988) recorded the crinoid taxon *Cupressocinites abbreviatus* Goldfuss from Big Bend and an indeterminate crinoid from Herveys Range outcrops of the Burdekin Formation. In more recent times Cook (1993a,b; 1997) has examined molluscs from parts of the Fanning R. Group, and Zhen (1994) and Zhen & Jell (1996) have formalised some of the rugose coral taxa. Zhen & West (1997) described some symbionts in both stromatoporoids and chaetetids from the Burdekin Formation.

AUSTRALIAN DEVONIAN STROMATOPOROID STUDIES.

Systematic and palaeoecologic work on Australian Devonian stromatoporoids is sparse. Stromatoporoids have been mentioned commonly, listed infrequently and described rarely. To date the works of Ripper (1933, 1937a,b,c,d, 1938), Mallett (1968, 1970a,b, 1971), and Cockbain (1984, 1985), Webby, Stearn & Zhen (1993) and Webby & Zhen (1997) form the main body of Devonian stromatoporoid work.

In Victoria, description of Early Devonian stromatoporoids from Lilydale (Ripper 1933, 1937b), Loyola (Ripper 1937c), Buchan (Ripper, 1937d) culminated in a synthesis of their assemblages by Ripper (1938). She also described '*Amphipora ramosa*' (Phillips) from Western Australia. The Lilydale, Buchan, Tyers and Waratah Bay stromatoporoids were reviewed by Webby, Stearn & Zhen (1993).

Mallett (1968, 1970a,b, 1971) described stromatoporoid faunas from the Broken R. Province. Cockbain (1984) described 25 species of stromatoporoids from the Canning Basin reef complexes, Western Australia. The taxa range in age from Givetian to Famennian. A small fauna of stromatoporoids from the Carnarvon Basin was described by Cockbain (1985). Shorter works include those of Etheridge (1911), Dun (in Benson 1918), Cockbain (1979) and Cockbain (1989). Webby & Zhen (1993) described the

Early Devonian allochthonous stromatoporoids of the Jesse Limestone, New South Wales. There are a number publications which list Australian Devonian stromatoporoids, including Benson (1922), Teichert & Talent (1958), and Philip (1960,1962). This summary does not include the large number of minor references that are of little taxonomic value. Several of these are listed in Flügel & Flügel-Kahler (1968). Most recently Webby & Zhen (1997) have published part of their ongoing work on the stromatoporoid faunas from the adjacent Broken R. Province.

PALAEOECOLOGY

Cook (1995) established 11 marine facies within the Big Bend Arkose and Burdekin Formation providing an ecostratigraphic framework for faunal study. Zhen & Jell (1996) established a broad, basin-wide model for the Fanning R. Group, representing the coral and sedimentologic associations. Here a more detailed ecological roles, inter-relations and responses to different environments of the stromatoporoids and other selected organisms preserved in the Big Bend Arkose and Burdekin Formation will be discussed under 5 headings:

1) Stromatoporoid shape, and shape groupings present in stromatoporoid-bearing facies.

2) Differences in shape groupings between related facies to establish whether zonation exists across reefoid facies, and to investigate which factors most strongly influence stromatoporoid shape.

3) Diversity in shape within individual stromatoporoid taxa.

4) Relationships between stromatoporoids and other organisms, assessed from intergrowth and overgrowth phenomena to determine if inferences of the physical environment can be made from such characteristics.

5) Community groupings of stromatoporoid and other faunal elements, their partitioning and overlap, their guild structure, and the role of individual taxa within the guild structure.

In addition the palaeobiogeographic affinities and relationships of the fauna are also discussed.

STROMATOPOROID SHAPE

Stromatoporoid shape was controlled by both ecologic and genetic factors (Kapp, 1975; Kershaw & Riding, 1980; Kershaw, 1981, 1984, 1990; Stearn, 1982a; Kano, 1990). Analysis of
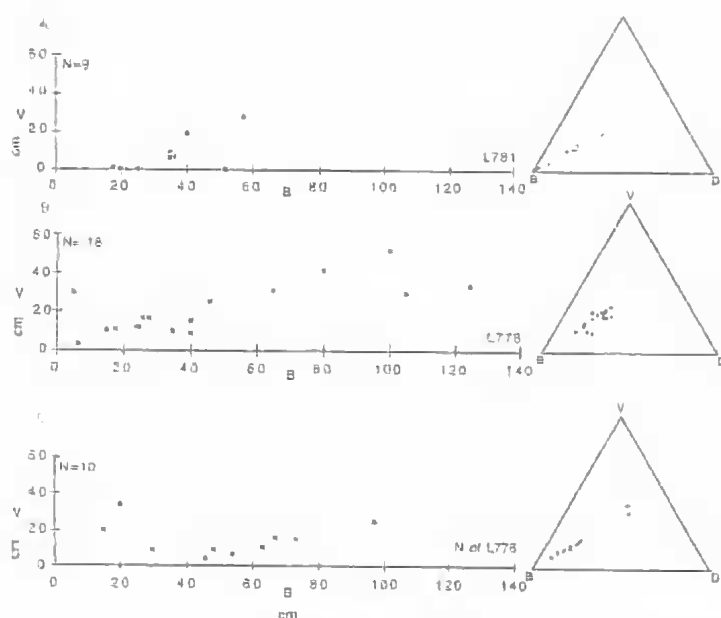
FIG. 2. Stromatoporoid skeletal morphology from patch reef environments of the Burdekin Formation. Bivariate plots show vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A. L781 patch reef approximately 23m above base of section. B. L778 patch reefs approximately 13m above base of section. C. Patch reef in spot exposure of facies approximately 1km N of L778.

developed by many authors including Broadhurst (1966), Abbott (1973), Kershaw & Riding (1978), Cockbain (1984), and Kano (1990). In this, and the following chapter dealing with the systematic descriptions of the fauna, the terminology of Kershaw & Riding (1978) is used, with the addition of 2 terms introduced by Cockbain (1984): 'stachyodiform' and 'amphiporiform'. Thus the terminology used herein is: laminar (with a height to base ratio < 1:10), low domical, medium domical, high domical (extended domical of Kershaw & Riding (1978)), bulbous, irregular, dendroid comprising stachyodiform and amphi- poriform.

Some authors (e.g., Kobluk, 1975; Kano, 1990) have attempted to graphically display the size groupings of stromatoporoids by use of a simple plot of width versus height. Although the procedure gives a good indication of size it was noted that it does not adequately quantify the shape of the organisms, leading Kershaw & Riding (1978) to parameterise stromatoporoid shape using percentile ratios of vertical height (V), basal width (B) and diagonal distance (D) at a set angle (q) plotted on a triangular diagram or triplot. For comparative purposes, their method provides a simple, quick, graphical display of shape domains within facies or communities. Kershaw & Riding's (1978) approach is quite useful in indicating the shapes of large, regular stromatoporoid skeletons and those of other groups. However the method has the following disadvantages: (1) There is no dimensional scale for the skeleton. (2) The entire field on the triplot is never represented as some forms are unattainable in stromatoporoids. (3) The method does not adequately represent dendroid forms and does not deal with irregular forms. (4) The method requires either full specimen collection, generally impossible with the Burdekin fauna, correction of 'oblique' data , or excellent, vertically exposed sections through the centres of skeletons.

skeletal growth shape may provide useful insights into the palaeoecology of fossil reefal and biostromal organisms, but there is little consensus on the precise influences of environmental conditions on shape. Many authors have made palaeoecological inferences based on the study of both gross colonial shape in relation to substrate (Kapp 1975, Kershaw & Riding 1978, Kershaw 1981, 1984, 1990, Bjerstedt & Feldmann 1985, Kano 1990), and relationships of colony margins to enclosing sediments (Broadhurst, 1966; Kapp, 1975; Kershaw & Riding, 1978; Kershaw, 1984). Several authors have argued for lateral and vertical zonation within stromatoporoid-bearing strata (Kobluk, 1975; Bjerstedt & Feldmann, 1985) and some have attempted to relate stromatoporoid shape groupings, to combinations of ecological conditions such as oxygenation, turbulence, and sedimentation rate (St Jean, 1971; Bjerstedt & Feldmann, 1985; Kano, 1990; Kershaw, 1990).

For a qualitative assessment of stromatoporoid shape it is important to maintain consistent terminology. Gross skeletal terminology has been

Nevertheless the triplot method of representing shape domains is a useful benchmark with which to compare stromatoporoid occurrences and combined with the more traditional base versus height plots, and provides a useful graphical characterisation for the assemblages. Data were collected from representative stromatoporoid-dominant facies to characterise the general shapes domains of the non-dendroid stromatoporoid fauna. Field measurements were made with a simple measuring tape, reading to the nearest 0.5cm.
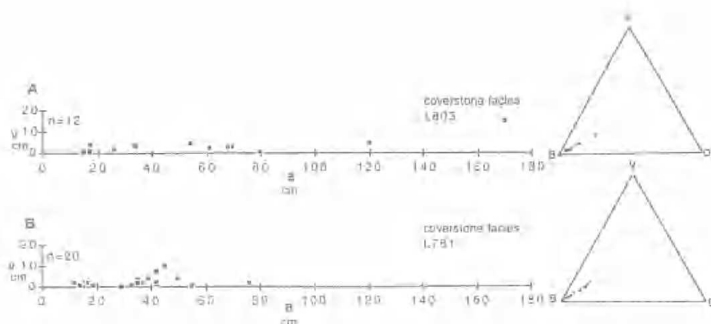

FIG. 3. Stromatoporoid skeletal morphology from coverstone facies of the Burdekin Formation. Bivariate plots show vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A, L803, uppermost facies exposed within Ropeladder Cave. B, L781, facies immediately underlying biohermal unit.

STROMATOPOROID SHAPE WITHIN PATCH REEFS. Two types of patch reefs were identified within the nodular limestone facies by Cook (1995); columnar, bulbous or pillar shaped reefs and diffuse patches of coverstone-framstone.

Both types show a dominance of large, low domical forms (Fig. 2) with very few high domical and bulbous forms. For the loosely bound, framestone and coverstone style of patch reefs these shapes can be attributed to the need for the stromatoporoid to grow more quickly laterally than vertically across a muddy substrate for support, thus distributing the weight across a larger surface area. This phenomenon has been noted by several authors (Meyer, 1981; Bjerstedt & Feldmann, 1985; Fagerstrom, 1987; Kano, 1990). The strategy was called the 'snow-shoe' approach by Bjerstedt & Feldmann (1985). Within the 'rauk' patch reefs the stromatoporoid skeletons are individually dominated by low domical forms, but their superposition creates the high relief profile of the patch reef. Away from these patch reefs and commonly in haloes around them, dendroid, mostly stachyodiform elements of the fauna are common.

STROMATOPOROID SHAPE WITHIN LAGOONAL PAVEMENTS. A number of coverstone occurrences were interpreted as lagoonal pavements either leeward of bioherms or within a biostromal complex (coverstone subfacies (Cook, 1995)). These pavements are almost exclusively composed of laminar to very low domical stromatoporoids (Fig. 3). Skeleton edge raggedness suggests moderate sedimentation rate (Broadhurst, 1966; Tsien in Stearn 1982a; Bjerstedt & Feldmann, 1985), which could not have exceeded rates within the nearer shore lagoons supporting patch reefs. Indeed, in the coverstone facies of L803, the laminar dominant forms occur at the top of an energy waning cycle suggesting a relative reduction in sedimentation. Control by substrate-type in addition to sedimentation rate is indicated, with growth forms reducing their weight per unit area (Kershaw, 1984; Bjerstedt & Feldmann, 1985; Kershaw, 1990). Some of the laminar forms in these occurrences are spectacularly thin in comparison to their width (Fig. 3). St Jean (1971) suggested that thin laminar forms occurred in oxygen poor conditions, but as Bjerstedt & Feldmann (1985) have argued, a laminar form would be at a disadvantage in such circumstances with the living surface close to the sediment-water interface. Furthermore, the extensive bioturbation, and the presence of molluscs and brachiopods suggest a moderately well-oxygenated benthos at L803.

Robustly dendroid skeletons are abundant in lagoonal pavement facies, attesting to the importance of the dendroid form in mud-dominated substrates. Bjerstedt & Feldmann (1985) argued that fasciculate skeletons are disadvantaged within this environment. Clearly the abundance of dendroid forms within the muddy facies of the Burdekin Formation refutes this argument. On the contrary, dendroid skeletons would be able to raise the living surface well above the sediment water interface. The only problem is
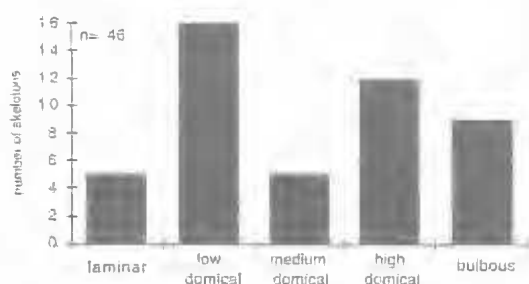
FIG. 4. Histogram showing proportions of gross skeletal shapes for compound skeletons from biostrome within fossiliferous siltstone facies at L788, approximately 16m above base of section.

to provide a substrate upon which to initially colonise, but the abundant small bioclasts of molluscan hash, small corals and other millimetre-scale debris would have been sufficient. As sedimentation progressed, the dendroid skeleton, becoming progressively more buried in the substrate, would gain stability.

STROMATOPOROID SHAPE WITHIN BIOSTROMAL OCCURRENCES. Several types of biostrome were identified by facies analysis in Cook (1995). These are generally the innermost shelf biostromes of the fossiliferous siltstone facies typically represented at L788, and the extensive proximal shelf biostromes represented throughout the Fanning R. area.

(1) Innershelf biostrome (JCUL788)

Study of this biostrome revealed that it was loosely bound, enclosed by dominantly siliciclastic facies, and formed in a shallow, subtidal environment, situated extremely close to shore in a restricted embayment with a moderate sedimentation rate as suggested by the sandy stringers and interbeds. In many ways this small biostromal lens, and the overlying 5 metres of stromatoporoid-bearing sequence, is one of the most instructive in the Burdekin sequences as it occurs in a facies with between 60 and 70% siliciclastic component (determined by bulk acid dissolution of several samples).

The dominant (>75%) gross skeletal shape is irregular, consisting of many compound forms with laminar and high domical components to the one skeletal unit. Others are multiply bulbous, arising from a low domical form. Of the 63 skeletons assessed in this biostrome only 48 could be assigned confidently to an approximate skeletal shape category (Fig. 4) and the size of the skeletons is highly variable. Unfortunately preservation is very poor, with much skeletal silicification, neomorphism and minor dolomitisation, rendering the taxonomy of this faunule difficult. The skeletons present are quite distinct from others in the Burdekin succession. The majority are compound, composed of repeated, variably thin layers of encrusting organisms including stromatoporoids, alveolitids and algae (see below). Their compound nature may explain the aberrant growth forms of the skeletons. If a single taxon adopted a limited and related range of growth forms (see below), then the superposition of many taxa in an encrusting relationship may be expected to produce a highly irregular form. Thus the skeletal form of most individual taxa within this biostrome is laminar, with thin encrustations complexly overgrown to form irregular compound skeletons. Away from, and within, the biostrome dendroid (mostly tabulate coral) skeletons are very common.
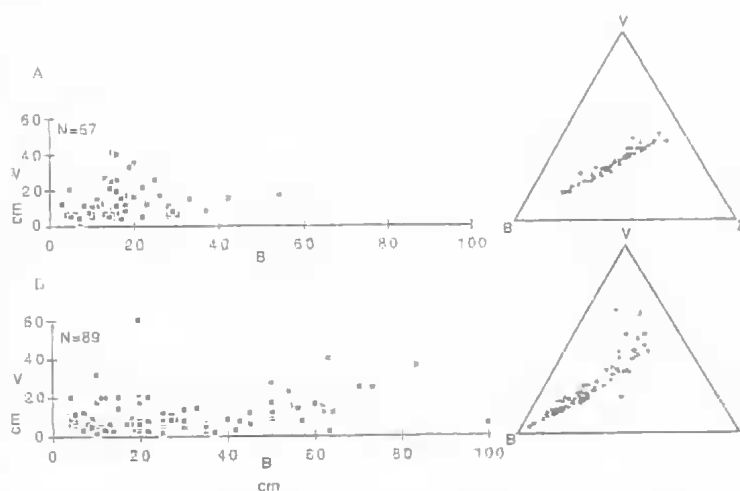
(2) Proximal shelf biostrome.

FIG. 5. Stromatoporoid skeletal morphology from proximal shelf biostromal facies of the Burdekin Formation. Bivariate plot showing vertical height (V) versus basal width (B) in centimetres. Triangular plots showing vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. A, L788 26m above base. B, L788 87m above base.

Stromatoporoids from the proximal shelf biostromal facies at L788 show a wide range of shapes and sizes, but with a general dominance of low to high domical forms, sporadic bulbous forms, and a lower proportion of laminar forms (Fig. 5) in comparison to the inner shelf. Compound skeletal phenomena are much less common. There are large numbers of fragmental skeletal remains within reworked facies but it is obvious that the unreworked facies do represent the stromatoporoid populations adequately.

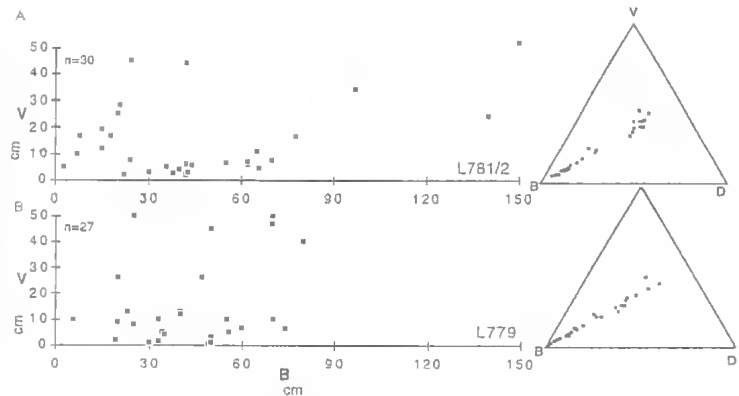Of the larger stromatoporoid skeletons, many show

FIG. 6. Stromatoporoid skeletal morphology from proximal shelf framestone facies of the Burdekin Formation. A, vertical height (V) versus basal width (B) in centimetres for L781/2 and L779. B, triangular plots of vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°.

directional growth changes, probably the result of in vivo reorientation. The marked dominance of higher forms in some units of the micritic stromatoporoid floatstone (Fig. 5) may indicate lower sedimentation rate, or a slightly reduced ambient energy (turbulence) away from shoreline. Bioturbation and the abundance of brachiopods negate low oxygen conditions. Sufficiently low energy ambient conditions coupled with a lower sedimentation rate on the mid-shelf would have enabled higher forms to be maintained on the substrate. Inability of some higher stromatoporoid skeletons to maintain a foothold may account for all the regrown high domical stromatoporoids in the facies with reorientation due to sporadic toppling.

Interstitial stachyodiform and amphiporiform taxa play a major role in the biostromes, with *Amphipora* dominating the muddy substrate, occupying patches between the larger stromatoporoids. In addition *Stachyodes costulata* is found as detached branches and as branches originating from an encrusting surface, demonstrating change in growth form within the one skeleton. There are no recorded attachment or encrustation habits of *Amphipora*. Perhaps this is a function of a small size of the attachment surface or perhaps the method of attachment was purely soft-part, but the latter possibility seems unlikely given the ability of *Euryamphipora* to encrust. Both dendroid taxa were successful between the larger stromatoporoid skeletons where they were sheltered, and able to raise the living tissue well above the substrate.

STROMATOPOROID SHAPE WITHIN BIOHERMS (REEFS). Well exposed outcrops of stromatoporoid framestone along the Burdekin R. (L779, L781, L782) allow for a sizeable analysis of stromatoporoid shape domains. The bioherm is dominated by low to medium domical forms (Fig. 6), many wider than 1m, and higher than 50cm. There is a general reduction in the number of high domical and bulbous forms in comparison to the biostromal facies in the Fanning R. area which may be a function of higher energy at the reef top, and the general difference in the stromatoporoid taxa between the 2 areas. Whilst common, the dendroid fauna is less abundant than in flanking environments, restricted to interskeletal niches.

STROMATOPOROID SHAPE WITHIN DISPERSED STROMATOPOROID PAVEMENTS AND OFFSHORE THICKETS. These environments were completely dominated by *Amphipora* and/or ramose tabulate coral taxa, and the role of the non-dendroid stromatoporoids was minor on the distal shelf. Growth form was variable, with some facies dominated by thick laminar and low domical forms (Fig. 7), both with and without ragged margins, and other occurrences showing sporadic medium and even high domical forms. The thick laminar and low domical forms occur in the dispersed stromatoporoid packstone facies which, given the abundance of micrite presumably derived from algae, would have been a highly productive carbonate factory where carbonate accumulation was relatively high, the overall substrate
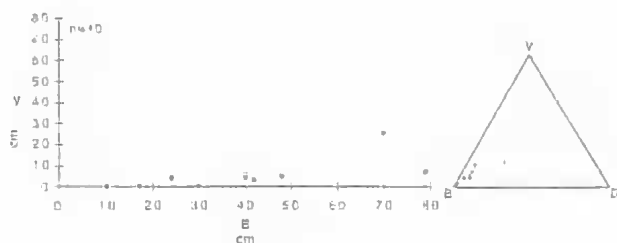
FIG. 7. Stromatoporoid skeletal morphology from dispersed stromatoporoid and coralline packstone facies of the Burdekin Formation. Bivariate plot shows vertical height (V) versus basal width (B) in centimetres. Triangular plots show vertical height (V), basal width (B) and diagonal distance (D) following the method of Kershaw & Riding (1978), with diagonal angle set at 25°. L781 units above framestone facies.

relatively soft, but with much millimetre-scale skeletal debris available on which to initially encrust. Sporadically preserved raggedness within higher forms of the coralline packstone facies suggeststhat these skeletons kept pace with carbonate accumulation following initial rapid lateral growth.

STROMATOPOROID SHAPE WITHIN SILTSTONE MICROATOLLS. Many stromatoporoids within this facies are encrusting in habit, thus having a laminar form, but there are a few low to medium domical forms, and sporadic high domical forms. *Clathrocoilona spissa* has an irregular, laminar shape in this facies. *Salairella buecheliensis* and *Stromatopora huepschii* show low to medium, rarely high, domical skeletons. The varying microenvironments around such *Endophyllum* accumulations would account for much morphological variation, and the laminar (encrusting habit) forms would result from strong competition for substrate control within an increasingly clastic environment.

SHAPE ZONATION

BURDEKIN RIVER. Laminar forms in the cover-stone facies of L779, and L781/2 are vertically succeeded by low-medium domical forms of the bioherm facies. This vertical zonation is strikingly obvious (Fig. 8) and cannot be related to faunal differences as the stromatoporoid taxa are common to both facies and dominated by *Hermatostroma maculatum* and *Gerronostroma hendersoni*. The progression is interpreted as one of self-generating change in the available skeletal

substrate. As the number of large skeletons increased, the skeletal substrate available for colonisation was enhanced, increasing the potential for frame-building. Thus the transition from laminar to domical dominant facies reflects the development from an encrusting pavement to a framework. A reduction is sedimentation rate is possible, but would have been affected by the development of a framework and the consequent elevated growth form of the reef surface from the surrounding substrate. Any change in turbulence would also result primarily from reef growth, rather than vica versa. Thus the major control on morphological change is substrate availability, with a feedback relationship between substrate and skeletal morphology.

FANNING RIVER CAVES. Brief mention has already been made in Cook (1995) of the sequence exposed in Fanning R. Caves (L803). The sequence is interpreted as a waning cycle commencing with a boulder rudstone zone composed entirely of reworked skeletons, an upper boulder rudstone with occasional in situ skeletons, a shingle zone with pebble- to cobble-sized reworked skeletons and many in situ skeletons with ragged margins, and an upper wackestone-coverstone zone dominated by extreme laminar forms. The shape progression in the upper 3 zones (Fig. 9) shows a reduction in the profiles of stromatoporoid skeletons mirroring the reduction in coarse skeletal debris, and hence hydrodynamic energy. Collection of material for taxonomic analysis was not possible as the caves are environmentally sensitive. However it is clear
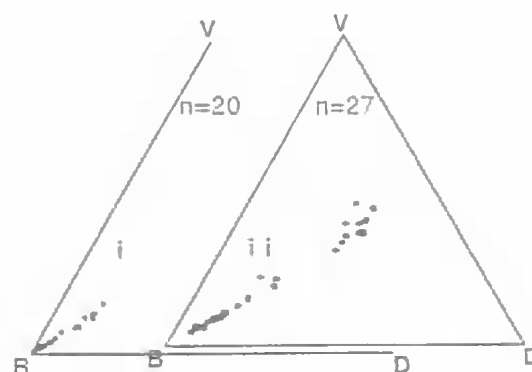

FIG. 8. Stromatoporoid shape domains using VBD triplot for coverstone to framestone facies L781.
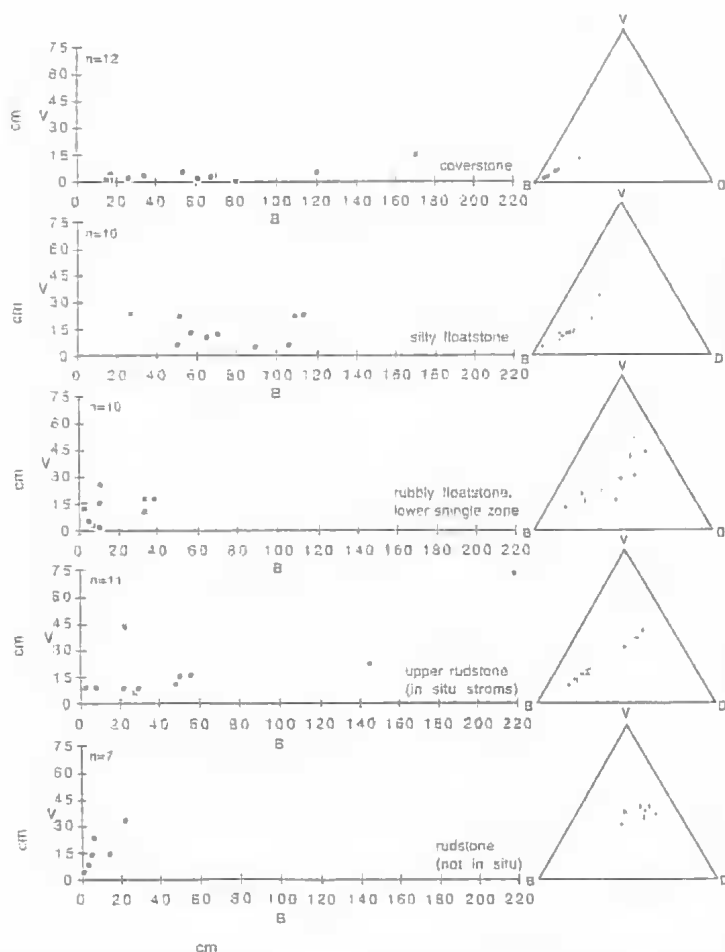
FIG. 9. Stromatoporoid shape change for measured section in Fanning River Caves L803 demonstrated in gross skeletal shape plots for each unit (coverstone at top).

domical in coverstone facies. Similarly *Hermatostroma maculatum* is laminar in coverstone facies and low-medium domical in the biohermal complex. Some taxa display a wide range of growth forms, from laminar to bulbous and irregular within the same facies. *Stachyodes costulata* had coexistent laminar, irregular and stachyodiform growth, indicating that it arose from an encrusting surface. Other taxa such as *Hermato-stroma episcopale*, strongly restricted to particular facies, are almost exclusively of one shape (laminar, less commonly low domical). Given that individual taxa display a range of shapes across, and within, specific environments, these data show there is very weak genetic control in addition to environmental controls outlined below.

CONTROLS ON SHAPE

The nature of the muddy substrate and the rate of sedimentation were fundamental determinants of skeletal shape within the inner shelf. Progression from laminar forms to low domical forms reflected in the transition from lagoonal pavement to bioherm was controlled by the increasing availability of skeletal substrate. In the biostromal complex, innermost dwellers had their irregular shape controlled by the sedimentation pattern, the encrusting strategy of the dominant taxa and the dominance of skeletal substrate. In the proximal shelf biostrome higher skeletal form reflected the quiet ambient conditions, sponsoring some toppling and regrowth.

OVERGROWTH RELATIONSHIPS

Although encrustation of individual stromatoporoid skeletons by other stromatoporoids and a range of other organisms is common, the phenomenon has been given little direct attention (Kazmierczak, 1971; Neild. 1986; Fagerstrom, 1987; May, 1993), although numerous authors have

from field inspection that there was no obvious change in the faunal constituents. The obvious change in gross skeletal shape demonstrates that here decreasing energy favours lower skeletal profiles. Bioturbation rules out the possibility of an oxygen-poor substrate and the thin forms can be attributed to moderate rates of sedimentation which periodically smothered the organisms.

STROMATOPOROID SHAPE AND TAXA

Stromatoporoid taxa within the Fanning R. Group display a range of shapes for individual taxa (Fig. 10). Most taxa, of which *G. hendersoni* is an example, are restricted to the low domical and adjacent growth forms. *G. hendersoni* is low to medium domical in form within the bioherm and biostromes, but is laminar to very low

Species \ growth forms	L	LD	MD	HD	BL	IRR	S	A
Actinostroma filitextum								
Atelodictyon fallax								
Gerronostroma hendersoni								
Gerronostroma sp								
Anostylostroma ponderosum								
Anostylostroma sp.								
Clathrocoilona abeona								
Clathrocoilona spissa								
Hermatostroma episcopale								
Hermatostroma ambiguum								
Hermatostroma maculatum								
Trupetostroma zheni								
Stachyodes crassa								
Stachyodes costulata								
Amphipora ramosa								
Amphipora pervasiculata								
Euryamphipora merlini								
Stromatopora huepschii								
Stromatopora sp								
Ferestromatopora heideckeri								
Salairella buecheliensis								
Salairella cf. S. cooperi								
Glyptostromides boiarschinovi								
Coenostroma burdekinensis								
Coenostroma wyatti								

FIG. 10. Gross skeletal shape ranges of major stromatoporoid taxa in the Burdekin Formation. L = laminar, LD = low domical, MD = medium domical, HD = high domical.

noted encrusting forms (Kobluk, 1975), habits and strategies. Many skeletons preserved within Devonian (and other) reefoid systems are compound units, made up of the superposed or overgrown skeletons of a number of organisms. These taxa are preserved either encrusted on the terminal surface of one taxon or included within the skeleton and later overgrown by regrowth of the original host or a subsequent encrusting organism. Kazmierezak (1971) interpreted 2 different surfaces within stromatoporoid skeletons: growth inhibition surfaces such as latilaminae bases, inclusion and regrowth surfaces and growth interruption surfaces such as those marked by encrusting tabulate corals. In the present work 2 types of surfaces are recognised with the encrusting relationships of biohermal and biostromal organisms (mainly stromatoporoids) of the Fanning R. Group. These are growth termination surfaces and growth interruption surfaces.

Growth termination surfaces are those within a compound skeleton which indicate that the older host has been completely encrusted by another organism. A growth interruption surface is a surface which shows partial encrustation of another taxon, but subsequent regrowth of the original host, or some other feature such as a latilamina base, which indicates a non-fatal growth pause.

The main skeletal encrusters, as distinct from sediment binders within the Fanning R. Group are: 1, Stromatoporoids: particularly *Clathrocoilona spissa*, *C. abeona*, *Stromatopora* sp., *S. huepschii*, *Gerronostroma* sp., *Ferestromatopora* sp., *Salairella bucheliensis*, and to a lesser degree *Hermatostroma maculatum*, *Gerronostroma hendersoni* and *Stachyodes costulata*. 2, Tabulate corals: foliose *Alveolites* sp., reptant *Aulopora* sp., and rare *Heliolites* sp. and *Aulostegites* sp. 3, Chaetetids: *Litophyllum koninckii*. 4, algae.

Most stromatoporoid skeletons within the Fanning R. Group are simple, consisting of 1 or 2 growth episodes with perhaps an encruster such as *Aulopora* sp. on the terminal surface. However it was initially observed that some facies contained a disproportionate number of compound skeletons which were more complex accumulations of many generations of encrusters in comparison to other stromatoporoid-bearing facies. In particular biostromes associated with the fossiliferous siltstone facies and lowermost silty rubbly biostrome facies included a high proportion of compound and irregular skeletons. To quantify this observation skeletons from 4 main biostromal and biohermal facies were surveyed in the field, in hand specimen and thin section, and ascribed to the following divisions of skeletal complexity:

a) simple skeletons: containing 1 or 2 taxa or growth phases with or without a minor terminal encrustation of auloporid coral.

b) skeletons of limited complexity: composed of 3 or 4 encrustations or growth phases

c) moderately complex skeletons containing between 5-7 phases of encrustation

d) extremely complex skeletons composed of more than 7 phases of encrustation.

Figure 12 highlights the large proportion of extremely complex skeletons within lowermost biostromes in the Fanning R. area (L788) whereas the most simple skeletons predominate in the
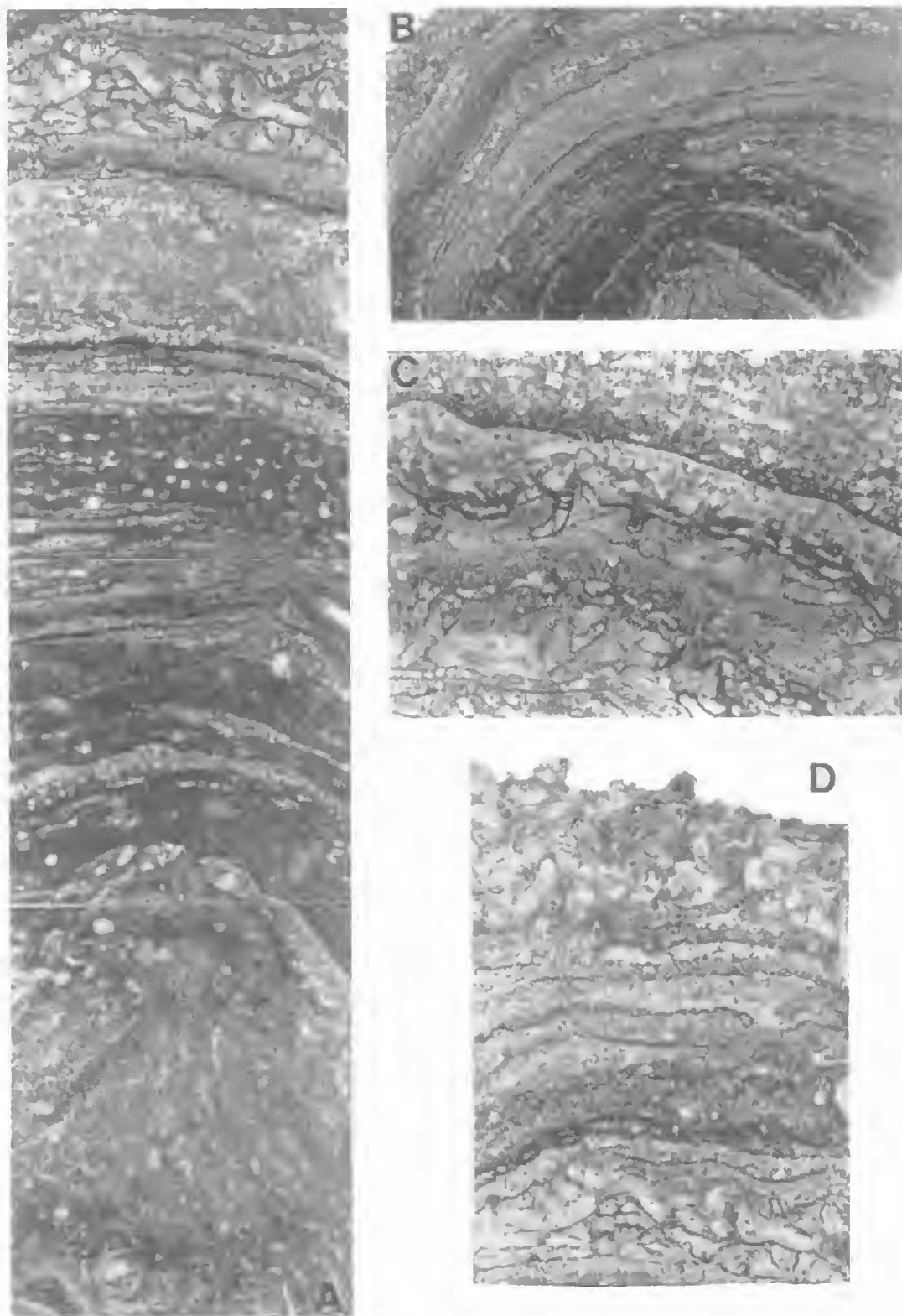
FIG. 11. A-D, thin sections of compound, complex skeletons from biostrome at L788/16m showing repeated overgrowths of stromatoporoids, tabulate corals and micritic seams ascribed to endolithic algae. A, D, F11426, × 5; B, F11426, × 2; C, F11430, × 5.

TABLE 1. Growth phase thicknesses for selected compound skeletons from the L788/16m nearshore biostrome.

Specimen JCUF	No. of phases	Thicknesses in mm	Taxa present
11420	7	10, 9, 9, 2, 4, 10, 7	*Stromatopora* sp., *Clathocoilona spissa*
11425	5	12, 3. 7, 6, 2	*Stromatopora* sp., *Clathocoilona spissa*, *Litophyllum* sp.
11423	8	1, 4, 1, 1, 7, 2, 7, 2	*Stromatopora* sp., *Clathocoilona spissa*, *Aulopora* sp.
11430	6	5, 3, 5, 6, 3, 3	*Stromatopora* sp.,*Clathocoilona spissa*, *Aulopora* sp.
11426	14	14, 1, 1, 5, 3, 6, 2, 2, 2, 3, 4, 3	*?Stromatopora* sp., *Clathocoilona spissa*, *Aulopora* sp.
11418	11	3, 3, 2, 6, 3, 6, 4, 5, 7, 2, 4	*Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa*
12772	13	18, 2, 3, 8, 2, 4, 15, 4, 1, 1, 2, 1	*Litophyllum* sp, *Stromatopora* sp, *Aulopora* sp., *Clathrocoilona spissa*
12773	9	20, 1, 5, 4, 3, 4, 5, 6, 8	*Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa*, *Alveolites* sp., *?Gerronostroma* sp.
12774	15	4, 3, 1, 3, 2, 12, 2, 1, 3, 1, 2, 4, 5, 5, 3	*Clathrocoilona spissa*, *Stromatopora* sp., *Alveolites* sp., *Aulopora* sp.
12775	10	2, 3, 4, 2, 2, 2, 1, 1,.4,.1	*Clathrocoilona spissa*, *Stromatopora* sp., *Aulopora* sp.
12776	11	3, 8, 1, 2, 2, 2, 2, 3,.2, 6, 6	*Stromatopora* sp. , *Aulopora* sp., *Clathrocoilona spissa*

biohermal facies of the Burdekin Downs area (L781).

Skeletons in the lowermost biostrome within the fossiliferous siltstone facies are referred to the *Clathrocoilona spissa-Aulopora* community. Skeletons are not only internally complex (Fig. 11), but also show a high degree of irregularity in gross shape. Phases of organism growth are thin, generally less than a few centimetres (Fig. 11, Table 1). This suggests that each growth phase was relatively short-lived. Termination surfaces between these phases are commonly marked by a thin dark micritic seam (Fig. 11) interpreted as having been produced by endolithic algae on the bare skeletal surface. By contrast the amount of sedimentary particles included between growth phases is relatively low. There is some marginal raggedness and sediment inclusion (Kershaw & Riding, 1978) but this is no more pronounced than in other facies, and many of the compound skeletons have an enveloping structure (*sensu* Kershaw & Riding, 1978). The biostrome in which these skeletons lived was a low-relief, poorly-bound pavement which developed adjacent to shore in a restricted, wholly subtidal, essentially siliciclastic environment. Acid residue analysis indicates that the siliciclastic component constituted between 60 and 70% of the enclosing detrital sediment of this facies, compared with variable, but much lower values for detrital sediment associated with other stromatoporoid-bearing facies (Table 2). Each encrustation phase within these complex skeletons represents a terminal surface. Extreme thinness of the growth phases suggests that they were relatively short-lived, or slow growing due to stress. Skeletons experienced succession of

short-lived encrustations punctuated by fatal conditions resulting from extreme stress.

Given the low frequency of sediment inclusions, these repeated fatal conditions are unlikely to result from suffocation by detrital sediment. In addition the abundance of the micritic seams supports the view that fatal conditions were succeeded by a period of skeletal exposure facilitating endolithic algal growth.

By analogy with similar phenomena in modern coralline systems under stress, these conditions were probably related to water quality conditions such as brackish water or hypersalinity. Given the much less common occurrence of complex skeletons in other facies, which have subdued siliciclastic signatures, the conditions were probably related to nearshore sedimentation, further suggesting spasmodic influxes of brackish water. Hence this biostrome is interpreted as a repeatedly stressed benthic community which was capable of quick regeneration. The phenomenon also graphically illustrates the high level of substrate competition within the community, as soon as skeletal surfaces were laid bare, they were encrusted.

Compared to biohermal and biostromal complexes, patch reefs developed in carbonate-dominated lagoons there appear to show a slight increase in the proportion of complex skeletons relative to simple skeletons, but the data set is too small for a firm conclusion. Too few data of this type are available from other Devonian reefoid systems to invite comparisons.

INTERGROWTHS

Intergrowths between stromatoporoids and other organisms have been recorded for over 150

TABLE 2. Percentage of acid insolubles, approximating percentage of siliciclastics for detrital sediment samples from selected facies of the Burdekin Formation.

Facies/ interpreted environment	Specimen JCUR	% Insoluble residue
Fossiliferous siltstone (adjacent to biostrome)	34942	69.9
	34943	61.7
	34945	66.7
Nodular limestone (adjacent to patch reefs)	32113	20.7
	32164	20.2
	32180	9.7
	32181	11.1
	32183	12.5
Silty floatstone or rudstone / nearshore biostromes (unsilicified detrital matrix)	34950	10.1
	34951	18.2
	35003	19.1
Floatstone / Biostrome (unsilicified detrital matrix)	34957	8.3
	34955	11.0
	34965	7.5
	35001	10.1
	35002	4.2
Framestone / Bioherm (unsilicified detrital matrix)	32120	5.8
	32165	30.3
	32169	15.6
	32170	24.3

years following the erection of *Caunopora* by Phillips (1841). Tabulate corals allied to the syringoporids are, undoubtedly the most common organism found as stromatoporoid intergrowths, but rugose corals, algae, calcareous worm tubes and ?gastropods have been documented as intergrowths within stromatoporoid skeletons. Intergrowths with stromatoporoids from the Burdekin Formation mirror this overall pattern with tabulate corals abundant and rugose corals common. Enigmatic spiral tubes also occur but are more sporadic. Zhen & West (1997) noted intergrowths of symbiotic worms within *Salairella* sp. and *Litophyllum konincki* and specimnes of *Helicosalpinx* sp. in *Hermatostroma* sp. from outcrops of the Burdekin Formation near Turtle Ck.

TABULATE CORALS. Earliest discussions of the caunopore state, the intergrowths of tabulate corals and stromatoporoids, date back to the introduction of *Caunopora placenta* of Phillips (1841). It was Roemer (1844), however, who first proposed caunopores to be the parasitic intergrowths of syringoporids and stromat-oporoids. Subsequent to this early work, there has been much discussion of the caunopore state, the history of which was reviewed by Mistiaen (1984). This contribution outlined the various coral genera which have been attributed to the caunopore state, and reviewed the generic (stromatoporoid) and stratigraphic occurrences

of such intergrowths. Tabulate corals intergrown with stromatoporoids have been assigned *inter alia* to *Syringopora* (e.g., Nicholson, 1886; Sleumer, 1969), *Syringoporinus* (e.g., Yavorsky, 1955, 1961) *Syringoporella* (e.g., Klovan, 1966; Birenheide, 1985) and *Caunopora* (Phillips, 1841; Birenheide, 1985).

Mistiaen (1984) reviewed the disparity between caunopore microstructure and that of *Syringopora*, casting doubt on the validity of assignment of caunopores to that genus. Subsequent authors have shown reluctance to refer caunopores to a tabulate genus, instead preferring ?*Syringopora* (Kershaw, 1987) or ?*Syringopora* cf. *vestita* Chudinova, 1971 (Young & Noble, 1989). An exception is Birenheide (1985) who assigned some caunopores to *Syringoporella*, and placed others within the portmanteau *Caunopora placenta* Phillips 1841. In line with Mistiaen's views, Birenheide also categorically stated that these caunopores are not *Syringopora*.

There are 2 types of stromatoporoid-tabulate coral intergrowths from the Burdekin Formation. Dominant are the regular intergrowths of a relatively small diameter, consistently-sized coral allied to *Syringoporella*? sp. (Fig. 13, A-D). Less common are the intergrowths of a slightly larger diameter tabulate coral more closely allied to *Syringopora* sp (Fig. 13 E-H.).

INTERGROWTHS OF *SYRINGOPORELLA*? SP. Such intergrowths are common and were found within the following taxa, in decreasing order of abundance; *Coenostroma wyatti*, *Stromatopora huepschii*, *Glyptostromoides boiarschinovi*, and *Salairella* sp. These are all taxa with discontinuous thick coenosteles within a relatively irregular network. There are no occurrences of this type of syringoporid within stromatoporoids with a regular pillar-laminar structure. *Syringoporella*? sp. was not found outside stromatoporoid skeletons.

Individual corallites found as intergrowths within all these taxa are 0.45-0.75mm in diameter , and corallite walls are relatively thick (mean = 0.140mm, s= 0.027mm, n=60). Tabulae within the corallites are scarce, but are thin and slightly concave upwards. Some samples show unequiv-ocal infundibuliform tabulae in addition to the slightly curved varieties. Data on corallite size and spacing (Fig. 14) show no significant variations between the different stromatoporoid taxa. It appears that syringoporid growth began in the early stages of the development of the
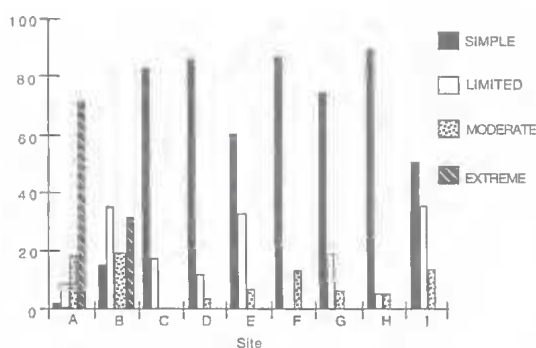
FIG. 12. Comparison of overgrowth occurrence in major stromatoporoid-bearing facies of the Burdekin Formation, showing percentages of simple skeletons, and those of limited, moderate and extreme complexity skeletons. A, fossiliferous siltstone facies, Fanning R., L788/16m n=63; B, fossiliferous siltstone facies, Fanning R., L788/22m n=26; C, biostromal facies, Fanning R., L788/60m n=24; D, biostromal facies, Fanning R., L788/75m n=29; E, dispersed stromatoporoid pavement, Horseshoe Bend, L787/ 200m n=16; F, patch reef, nodular limestone facies, Burdekin Downs, L781/25m n=15; G, grainy floatstone subfacies, Fletcherview, L778/25m n=48; H, framestone subfacies, Burdekin R., L781/30m n=200; I, *Endophyllum* siltstone facies, Fanning R., L788/ top of sequence n=14.

stromatoporoid colony, and its lateral development matched that of the host resulting in the distribution syringoporids throughout entire specimens of stromatoporoid. The syringoporid corallites are nearly always perpendicular to stromatoporoid coenostromes, unlike distributions illustrated by Young & Noble (1989: fig. 3a,b,d).

The corallites bud by the extension of stolons, approximately one third the diameter of the corallite, which arch gently upwards 1 or 2 stromatoporoid laminae distant from their origin. Surrounding each syringoporid corallite is a thin sheath of stromatoporoid skeletal material, up to 0.2mm thick and coenostromes upwardly inflect where they meet the corallite wall.

Data on the tangential distribution of individual corallites was collected by measuring 'nearest neighbours'. In each thin section individual corallites were selected and the distances to the nearest 4 corallites was measured. These data show little variation in the spacing between adjacent corallites; in tangential section the syringoporids are extremely regular in their distribution across the stromatoporoid colony (Fig. 13A,D).

DISCUSSION. Young & Noble (1989) suggested that syringoporid growth within stromatoporoid skeletons was constrained by skeletal density of the host. All the taxa with *Syringoporella*? sp. intergrowths have comparable skeletal density, and possess a moderately irregular skeletal architecture. Host selection of stromatoporoids by corals was suggested by Kershaw (1987) who observed that ?*Syringopora* sp. occurred in only one taxon of stromatoporoid from Hemse, Gotland, Sweden. Unlike the present study, Kershaw's intergrowths were described from a host taxon with a regular pillar-laminar skeletal grid.

Young & Noble (1989) considered that the living syringoporid polyp was maintained at or just above the stromatoporoid growth surface. If the latter were true, then part of the side of the coral skeleton would be exposed to algal micritisation. Given that there are no micrite rims on the corallites, they must have been maintained at the same growth level as the stromatoporoid soft tissue surface. Upward inflection of stolons reflect the need to maintain upward growth with the growth of the stromatoporoid.

The secretion of stromatoporoid skeleton around the corallites suggests a response to the syringoporids presence by the stromatoporoid soft tissue and may suggest an advantage of structural support being afforded the coral. It also suggests likely soft-part contact, given the interpreted level growth surface for both organisms.

Regular growth would suggest a mutualistic rather than a detrimentally parasitic relationship. Coral preference for stromatoporoids of a particular skeletal style would support a non-infestation relationship. The equivalence of growth surface for both organisms suggests there was no additional substrate advantage for the coral over the stromatoporoid. Kershaw (1987) noted that syringoporid intergrowths from the Silurian of Gotland were most common in high-energy, shallow water facies. In the Burdekin Formation *Syringoporella*? sp. intergrowths are most common in distal shelf facies, but this is most probably due to the preference of host taxa for these environments.

Whether the relationship between the stromatoporoids and corals was one of mutualism, commensalism or parasitism will remain unresolved until preserved soft parts are discovered. Nevertheless parasitism is rejected given the lack of detrimental effect on the stromatoporoid.
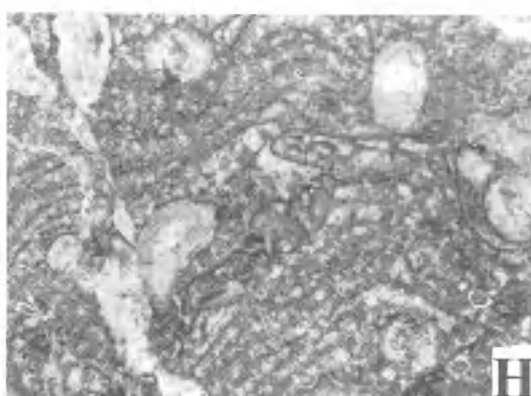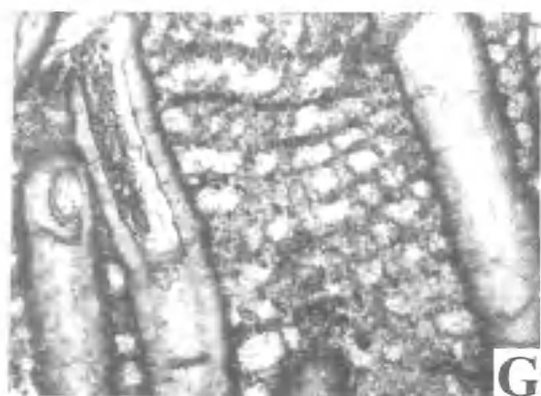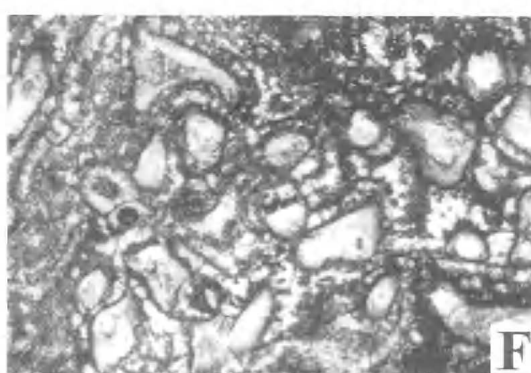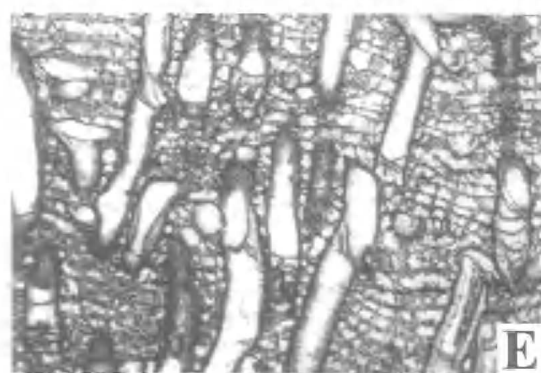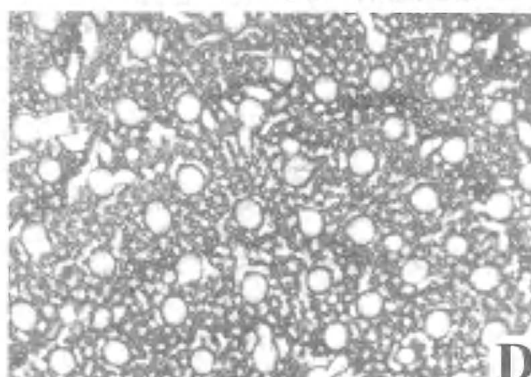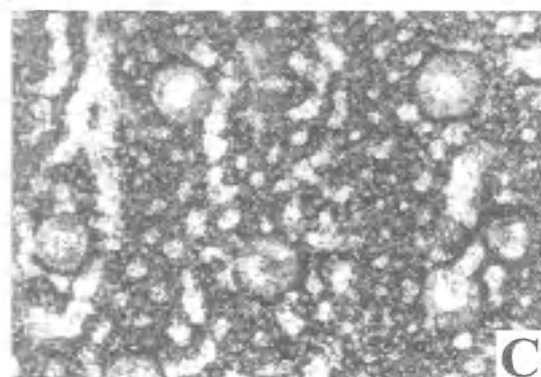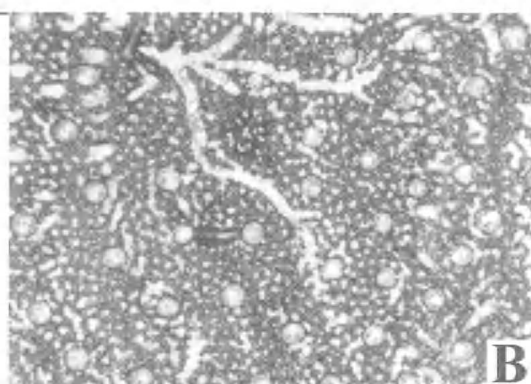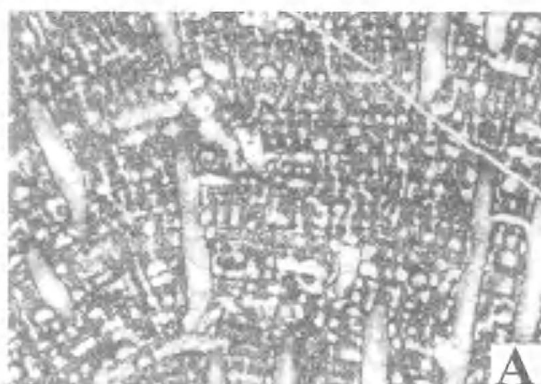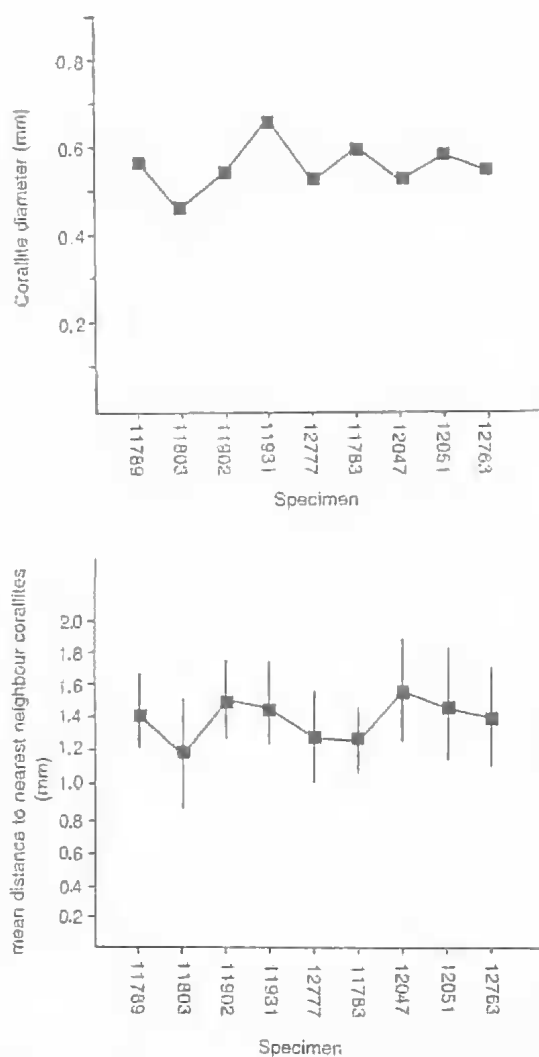
FIG. 14. Corallite diameter and spacing for intergrowths of *Syringoporella?* sp. n=30 for each specimen.

Problems with the affinity of the caunopore organism have been raised by Mistiaen (1984) based on studies of ultra-thin microstructure of the corallite wall. Kershaw (1987) noted significantly different microstructures in caunopores than those of Mistiaen (1984) and most authors (e.g., Kershaw, 1987; Young &

Noble, 1989) note that intergrowth syringoporids differ from those coexistent outside stromatoporoid skeletons. It is likely, given the relationship of syringoporid skeletal material within stromatoporoids, that both macro and microstructural modification took place.

The second variety of stromatoporoid-tabulate coral intergrowth is less common. The corallites are larger than *Syringoporella?* sp., have definite infundibuliform tabulae, thinner corallite walls and are not as regularly distributed in the host. These are known from *Hermatostroma episcopale* and *Gerronostroma* sp. Growth initiated near the base of the skeleton but was not regular or consistently oriented throughout the skeleton. The taxonomic affinities of this form are uncertain, but its gross morphology invites comparison with *Syringopora*.

RUGOSE CORALS. A number of taxa, including *Gerronostroma* sp., *Stromatopora* sp., *Hermatostroma maculatum* and *Gerronostroma hendersoni* contain sporadic rugose coral intergrowths, including *Disphyllum* sp., *Stringophyllum* sp. and other unidentified rugose coral taxa (Fig. 15A-D). They mostly occur as isolated corals within the stromatoporoid skeleton, but a few stromatoporoids contain moderate numbers of rugose corals. They are not regularly distributed throughout the skeleton, often have a dark micritic line at the edge of the coral, and the stromatoporoid laminae inflect upwards against the coral wall in vertical section and the skeletal structure wraps aroundFig. 14. Corallite diameter and spacing for intergrowths of *Syringoporella?* sp. n=30 for each specimen. the coral. Coral growth is commonly oblique to stromatoporoid growth layers. The presence of the marginal micrite envelope suggests that the rugose coral grew at a level above the stromatoporoid surface, thus enabling endolithic algae to infest the exposed corallite skeleton. In this way the coral is exploiting the stromatoporoid skeleton as substrate and for structural support. The random growth orientations suggest fortuitous rather than deliberate intergrowth.

OTHER ORGANISMS. Helical-spired tubes allied with *Helicosalpinx* sp, are sporadic within

FIG. 13. Tabulate coral intergrowths with stromatoporoids from the Burdekin Formation. A-D, intergrowths of *?Syringoporella* sp. with *Coenostroma wyatti* sp. nov. A-C. F12763. A. vertical section, × 5; B, tangential section, × 5; C, tangential section. × 15; D, F11783. tangential section, × 5. E-H, intergrowths of *Syringopora* sp. E-F, F12678, *Gerronostroma* sp.; F, vertical section, × 5; E, tangential section, × 5; F, vertical section, × 15; H, F11870, *Hermatostroma episcopale* Nicholson, tangential section. × 5.
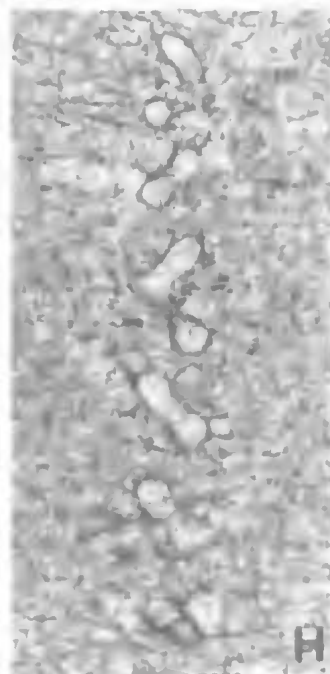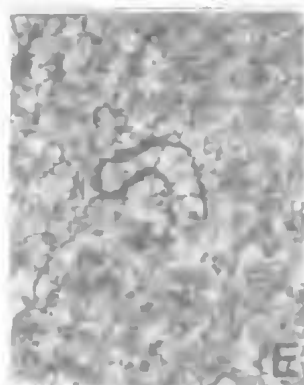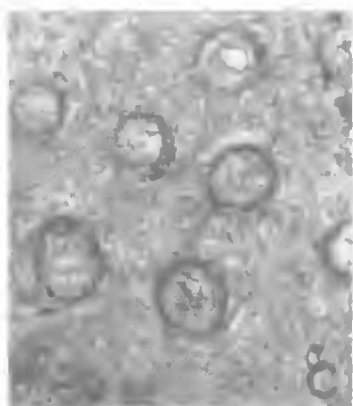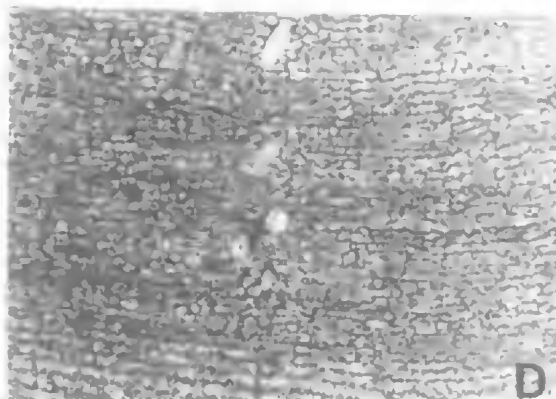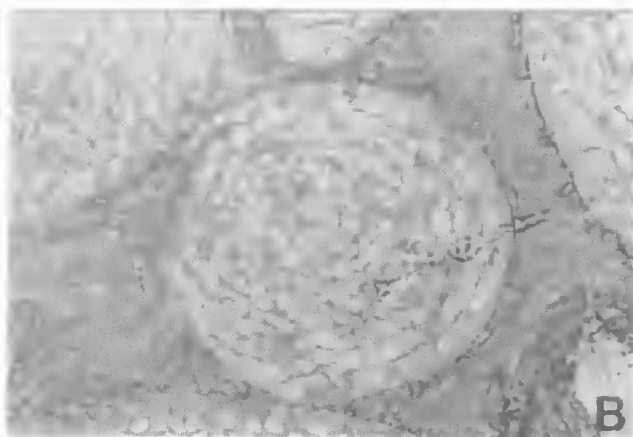
many stromatoporoid taxa (Fig. 15 E-H) and the massive tabulate coral *Alveolites* sp. cf. *A. intermixtus*. These are found most commonly within specimens of *Actinostroma filitextum*, *Gerronostroma hendersoni* and *Gerronostroma* sp. Such tubes have been allied to the Vermes (Plusquellec, 1968a,b; Oekentorp, 1969), and possibly gastropods (Cockbain, 1984). Some have thin partitions (Fig. 15) confirming that the organism sealed its living chamber. Such partitions led Cockbain (1984) to suggest septate gastropods were possibly inquilinistic in habit. Zhen & West (1997) concluded that a live-live interaction took place between unnamed worms and *Salairella* and *Litophyllum*.

STROMATOPOROID AND OTHER COMMUNITIES OF THE FANNING RIVER GROUP

One of the fundamental aims of this work is to discuss the association of faunal elements in relation to the various interpreted environments of the Fanning R. Group. I have not dealt in detail with the rugose corals, save cursory identifications following Zhen (1991) who described a number of rugose coral associations for the group. Rigorous taxonomic attention has not been given to the large tabulate coral fauna; rather open nomenclature identifications suffice for this study. The stromatoporoid composition of each fauna is variably dependant on the quality of preservation which greatly determines the identifiablity of individual stromatoporoid specimens. Of the approximately 1000 specimens of stromatoporoids collected, slightly less than one half were identifiable in thin section. Some areas, especially Kirkland Downs and Mount Podge, contained stromatoporoid faunas that were unidentifiable due to diagenesis.

The taxa described below and key additional taxa are tabulated relative to facies groupings (Table 3). On the basis of this, 10 communities are recognised for the Group based on the stromatoporoid-tabulate coral-and molluscan faunas: 1) *Burdikinia*; 2)*Modiomorpha*; 3) *Stachyodes-Syringopora*; 4) *Clathrocoilona*

spissa -Aulopora; 5)*Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus*; 6) *Hermatostroma maculatum-Gerronostroma hendersoni*; 7) *Coenostroma-Hermatostroma episcopale*; 8) *Amphipora pervesiculata*; 9) *Endophyllum* community; and, 10) cephalopod association (not in situ).

GUILD STRUCTURE

Fagerstrom (1987) demonstrated the general utility of the guild concept to reefs, both modern and ancient. He defined 5 major guilds within the reefal environment; constructor, binder (encruster), baffler, dweller and destroyer, in order to account for the spatial and resource organisation of reefs. The constructor guild is the most important to the reefal ecosystem, its 'vigorous expression' being a necessary condition for reefal community development (Fagerstrom, 1987:203). Whereas this guild concept is readily applied to reefs (sensu framestone-type bioherms), problems in the role and definition of guild states arise when the concept is applied to biostromal deposits which, according to Fagerstrom (1987), are not true reefs. Clearly most of the general concept of reefal guilds can be transferred to biostromal communities, but the biostromal guild structure differs in the role of binders or encrusters, and the equivalent of the topographic relief-producing constructor guild. Although the organisms are similar, and in some cases involving identical taxa, the organisms are commonly isolated, or only partially bound to their neighbours. Therefore the use of 'constructor', in the sense of building a reef with topographic relief, is somewhat of a misnomer when applied to biostromes. Fagerstrom's (1987) binder (encruster) guild included organisms which encrusted other organisms and the sediment, thus binding the reef framework together. In biostromes the encrustation of larger organisms and the binding of sedimentary substrate are often performed by different organisms. For instance it is difficult to reconcile placing auloporid corals encrusting a larger skeleton in the encruster guild with laminar stromatoporoids which cover a surface of muddy

FIG. 15. A-C, rugose coral intergrowths with stromatoporoids from the Burdekin Formation. A, F11892, *Gerronostroma* sp. with rugose corals, × 5; B, F12016, *Gerronostroma* sp. with rugose corals, × 6; C, F11892, tangential section, × 5. D-H, 'vermetid' intergrowths within stromatoporoids from the Burdekin Formation. D, F11939, *Actinostroma filitextum* Lecompte, 1951, vertical section, × 6; E, F11892, *Gerronostroma* sp. with partitioned commensal, vertical section, commensal is oriented obliquely, × 15; F, F11936, *Actinostroma filitextum* Lecompte, 1951, tangential section, × 20; G, F11879, *Actinostroma filitextum* Lecompte, 1951, tangential section, × 20; H, F11892, *Gerronostroma* sp., vertical section, × 15.

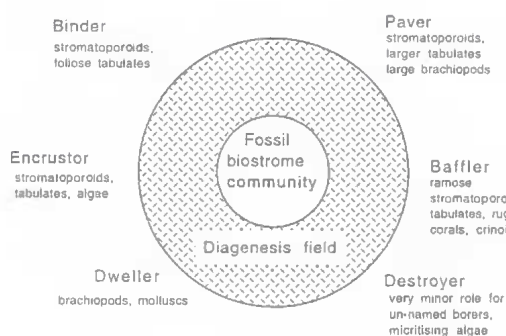| Taxa / Facies of Cook (1995)	abraded bioclast coarse siliciclastic	fossiliferous sandstone	fossiliferous siltstone	biostrome in fossiliferous siltstone	nodular limestone	patch reefs in nodular limestone	coverstone	biohermal facies	stromatoporoid biostromal facies	dispersed stromatoporoid packstone	coralline packstone	Endophyllum siltstone	micritic carbonate
1. Actinostroma filitextum								•					
2. Aculatostroma? sp.											o		
3. Clathrodictyon sp.								o					
4. Atelodictyon fallax				?				•	•				
5. Schistodictyon sp.					o								
6. Gerronostroma hendersoni				?	o	•	•	•	o		•		
7. Gerronostroma sp.				•				•	•				
8. Anostylostroma ponderosum								•					
9. Anostylostroma sp.									•				
10. Gen. Et sp indet cf. Clathrodictyella								o					
11. Stictostroma sp.										o			
12. Clathrocoilona abeona						•		•			•		
13. Clathrocoilona spissa				•								•	
14. Hermatostroma episcopale									o	o	•	•	
16. Hermatostroma maculatum						•	•	•	•				
16. Trupetostroma zheni			•		•								
17. Stachyodes crassa					o								
18. Stachyodes costulata	o	o	•		•	•	•	•	•	o	o		
19. Stachyodes sp. A											o		
20. Stachyodes sp. B										o			
21. Amphipora ramosa									•				
22. Amphipora pervesiculota										•	•		
23. Eurymphtpora merlini							•	o		o	•		
24. Stromatopora huepschii						•			•	•	•	•	
25. Stromatopora sp.				•					•				
26. Pseudotrupetostoma ambiguum									o				
27. Ferestromatopora heideckeri				•					•	•			
28. Salairella buecheliensis								•		•	•	•	
29. Salairella S. cooperi									•				
30. Solairella sp.											•		
31. Glyptostromides boiarschinovi										•	•		
32. Taleastroma sp									o				
33. Coenostroma burdekinense								o		•	•		
34. Coenostroma wyatti										•	•		
35. Parallelopora? Sp.							•	•					
MOLLUSCS													
Burdikinia burdekinensis	•	•	o										
Amphelissa carinotum	•	•	o										
Labrocuspis nodosa	•	•	o										
Fletcherviewia septata		•											
Modiomorpha mitchellae			•										
Phenacocyclas pohli								•					
Tanaodon louderbacki	•	•											
TABULATE CORALS													
Heliolites sp.			•				•	•	•	•	•	•	
Cladopora sp.			•	•	•		•	•	•	•	•	•	o
Alveolites sp.	o	o	•	•	•	•	•	•	•	•	•	•	
Aulopora sp. (laminar)			•	•	•	•	•	•	•	•	•	•	
Svringapora sp			•	•	•		•	•	•	•		•	
Romingeri sp.			•	•	•		•						
Thamnopora sp.	o	o	•	•	•							•	
Litophyllum koninchi (Chaetetid)				•	•	•	•	•	•	•	•	•	
Brachiopods (general)			•	•	•		•	•	•	•	•	•	
atrypids			•						•	•	•	•	o
Stringocephalus sp									•				

FIG. 16. Potential guild structure for Middle Devonian biostromes of the Burdekin Formation, modified from the reefal guild structure of Fagerstrom (1987).

carbonate sediment. Hence it is proposed, that in discussing the guild structure of level bottom biostromes (as opposed to bioherms) the guild group 'paver' be recognised to describe large constructor-equivalent organisms, and that 'binders' be recognised as the sediment coverers as distinct from the 'encrusters' of large skeletons. Bafflers, dwellers and destroyers remain herein as defined by Fagerstrom (1987). Thus the potential guild structure of the biostrome is given below (Fig. 16). The guild membership is listed for each community, as appropriate, below.

BURDIKINIA COMMUNITY. *The Burdikinia* community is a mollusc-dominated fauna which occurs within abraded bioclast coarse siliciclastic facies, fossiliferous sandstone facies and impure limestone facies, generally at the base of the Fanning R. Group, and within clastic intercalations throughout the carbonate sequence. The assemblage thrived on the coarse clastic, often turbulent, shoreface and in shallow inner shelf environments.

Four molluscan taxa dominate the assemblage; the gastropods *Burdikinia burdekinensis* (Etheridge, 1917), *Amphelissa carinatum* (Heidecker, 1959), *Labrocuspis nodosa* Heidecker and the bivalve *Tanaodon louderbacki* Kirk, 1927. In addition there is a fourth rarer gastropod *Fletcherviewia septata* Cook, 1993, scattered tabulate corals, the common rugose coral *Temnophyllum* sp. and sporadic *Stachyodes costulata* Lecompte complete the assemblage. At Fletcherview L778, characteristic trace fossils

(see Cook, 1993a) provide a useful insight into the molluscan assemblage.

The mobile sandy substrate would have been a habitat particularly attractive to the gastropods. Algal grazing would have been restricted in the more offshore coralline-stromatoporoid banks where available non-muddy substrate was occupied by stromatoporoids and coralline forms. Mud-dominant lagoons would have provided additional problems due to the large size (hence weight) of the shells. Because the gastropods were thick-shelled and fairly heavy, they were well suited to this high energy environment. There were 2 main strategies for dealing with turbulent conditions on the habitat. All 4 gastropods are heavy forms, but *Burdikinia, Labrocuspis and Amphelissa* are all compact, relatively low-spired, robust forms. *Labrocuspis* has been interpreted by Kase (1989) to have 2 modes of life; creeping over the substrate and partly infaunal. This second partly buried life mode may have been a strategy for dealing with high turbulence conditions.

MODIOMORPHA COMMUNITY. This community could be considered a variant of the *Burdikinia* community, as many of the elements are common to both. It occurs in the much abbreviated representation of Burdekin Formation near Boundary Ck, Paynes Lagoon Station and consists of in situ conjoined *Modiomorpha mitchellae* Cook, with minor *Burdikinia, Labrocuspis, Thamnopora* sp, and rare rugose corals. Modiomorphs are partly infaunal epibyssate suspension feeders with the gape protruding from the substrate (Bailey, 1983). The community is dominated by the modiomorph with subordinate coral bafflers.

STACHYODES-SYRINGOPORA COMMUNITY (Table 4). Baffler guild organisms overwhelmingly dominate this community which is largely exclusive to soft, muddy-bottomed, innershelf, impure bays and lagoons. The role of pavers on the lagoon floor in this impure environment was limited. Patch reefs developed as small 'rauks' or low biohermal accumulations within these bays and are not included in this community. *Stachyodes costulata* is the ubiquitous faunal element, the robustly dendroid tabulate *Thamnopora* sp. is abundant. Solitary rugose corals are generally of the '*Charactophyllum* sp.' type, showing the low,

TABLE 3. Distribution of stromatoporoid and other key taxa within facies of the Big Bend Arkose and Burdekin Formation. 1. Occurs as encrusting fauna and within boulder interstices. ◑ - rare, ● - common.

TABLE 4. Faunal components and guild status, of the *Stachyodes- Syringopora* community, with dominant forms in bold.

Bafflers	Pavers	Encrusters	Dwellers
Stachyodes costulata	*Litophyllum koninckii*	*Stachyodes costulata*	**Charactophyllum** sp.
Syringopora sp.	*Gerronostroma hendersoni*	*Aulopora* sp.	*Pseudomicroplasma* sp.
alveolitids			*Disphyllum* sp.
Stachyodes crassa			bivalves
Trupetostroma zheni			brachiopods
Romingeria sp.			?algae
branching alveolitid			

cup-shaped form better suited to muddy substrate and sediment expulsion as discussed by Zhen (1991). Another common rugose coral is *Pseudomicroplasma australe* (fide Zhen, 1991). Two very common tabulate coral elements are *Romingeria* and *Syringopora*. Both had a bushy rather than encrusting growth strategy within the impure inner shelf. This community is dominated by bushy forms capable of gaining height above the muddy, substrate. Abundant molluscan hash associated with this community suggests a large population of small, as yet, unidentified bivalves.

At 2 localities members of this community are found in facies representing preserved headlands. Common encrusting *Alveolites* sp. and *Stachyodes costulata* are found as interstitial fauna, and show negligible transport. These elements adopted an encrusting and interstitial strategy to enable them to exploit the barely subtidal rocky headlands. It appears that this fauna was restricted by substrate relief to where turbulence and sedimentation rate were enhanced, and the substrate too mobile to allow larval settling and growth. However *Stachyodes costulata* and *Alveolites* sp. are found as part of a rare fauna within facies interpreted as marine headlands where both are found as unabraded branches. *Stachyodes costulata* is also found encrusting granite boulders and cobbles. This relationship is interpreted to represent encrustation of boulder interstices, which afforded some protection in a high energy environment. Within reefoid environments elements of this community were reduced to interstitial, subsidiary roles, and the decrease in importance of *Stachyodes* and *Thamnopora* sp. was progressive across the shelf. Seaward of the biohermal complex, this community was not able to compete with that dominated by the more delicate *Amphipora* and *Cladopora*. The taxa of this community clearly were more successful on the muddier substrates due to their ability to grow above the seafloor. By inference it may have been more tolerant of siliciclastic input than other dendroid forms found within more offshore facies.

CLATHROCOILONA SPISSA-AULOPORA

COMMUNITY (Table 5). This community is best known from the Fanning River area and is dominated by encrusters and bafflers. It is perhaps the most unusual of the stromatoporoid assemblages in the Fanning River Group. It inhabited low, loose biostromes and pavement biostromes located within the impure muddy bays and lagoons of the innermost shelf representing environments dominated by fine-grained siliciclastics A large majority of skeletons within this environment are compound, containing overgrowths of a number of tabulate, stromatoporoid, rugose coral and algal taxa. The skeletal growth form is variable and irregular in profile but ranges in overall shape from laminar to bulbous, as previously discussed. Encrusters gained purchase on small coral or stromatoporoid fragments and skeletons developed as a series of overgrowths. Baffler elements are dominated by alveolitid corals including *Thamnopora* sp., rugose corals including *Disphyllum* sp., *Grypophyllum* sp, and minor *Stachyodes costulata*. Community composition reported below was biased by the general poor state of preservation of stromatoporoids in facies containing this community. Pervasive neomorphism and silicification has rendered many specimens unidentifiable. It is likely that *C. spissa* dominated the innermost shelf due its

TABLE 5. Members of *Clathrocoilona spissa- Aulopora* community and their proposed guild designations. Dominant taxa shown in bold.

Encrusters	Pavers	Bafflers	Dwellers
Clathrocoilona spissa	*Stromatopora* sp.	**Thamnopora sp.**	*Syringopora* sp.
Stromatopora sp.	*Gerronostroma* sp.	*Cladopora* sp.	rugose corals
Ferestromatopora heideckeri	*Stachyodes costulata*	*Stachyodes costulata*	gastropods
Gerronostroma sp.	unidentifiable		bivalves
Aulopora spp.	stromatoporoid		brachiopods
Litophyllum koninckii	*Heliolites* sp.		
algae			
encrusting alveolitid			

TABLE 6. Members of *Ferestomatopora heideckeri- Amphipora ramosa-Stringocephalus* community and their proposed guild designations. Dominant taxa shown in bold.

Pavers	Bafflers	Encrusters	Dwellers
Ferestramatapora heideckeri	**Amphipora ramosa**	Clathrocoilona spissa	other rugose corals
Atelodictyon fallax	Cladopora sp.	Stromatopora sp.	brachiopods
Gerronostroma sp.	**Dendrostella trigemme**	Alveolites sp.	**Stringacephalus sp.**
Stromatopora sp.	Cladopora sp.	Aulopora sp.	molluscs
Salairella cf. S cooperi.	Thamnopora sp.		
Gerronostroma hendersoni	Stachyodes costulata		
Litophyllum koninckii			
Heliolites sp.			

greater ability to rapidly encrust exposed skeletal surface and was slightly better tolerance of fine-grained siliciclastic input and its associated effects. *Aulopora* abundance was controlled by hard substrate availability.

FERESTROMATOPORA HEIDECKERI-AMPHIPORA RAMOSA-STRINGOCEPHALUS COMMUNITY (Table 6). This community dominates the biostromal complex, and is best known in the Fanning River area. It inhabited a wide zone ranging from nearshore to carbonate-dominant proximal shelf within extensive biostromal banks of very low relief. The substrate was highly variable, ranging from micritic muds to rubble with dendroid forms better preserved on, and presumably having preferred, the muddier substrates. The community is dominated by low to medium domical forms, and an abundance of delicate dendroid faunal elements. The large brachiopod *Stringocephalus* sp. is a common component, sporadically so abundant as to dominate local biostrome faunas. Given their large size, abundance and concentration into clumps they are probably a rare example of brachiopod which

could be considered as a paver guild member. The composition of this fossil community varies both laterally and vertically, and is best expressed within the carbonate dominated, proximal shelf facies. Occurrences of the community lower in the sequence are largely lacking in *Stringocephalus*, the first occurrence of this brachiopod being 27m above the base of the sequence within the type section. Lower occurrences also commonly show reduced numbers of *Amphipora*, the taxon being replaced by higher numbers of *Stachyodes costulata*. Biostromal units occur to the north of Fanning River (L789), where stromatoporoids and corals numbers are significantly reduced and large concentrations of *Stringocephalus* sp. dominate.

The community is clearly dominated by the baffler and paver guilds. Stromatoporoids and other pavers are closely spaced within patchy zones, with the abundant baffler and dweller fauna interstitial and between patches. The encruster guild is less dominant within this community. Taxa which in other communities are important encrusters are more prevalent as pavers within this biostromal environment. Preservationally this community is affected by common obliterative neomorphism and silicification rendering many stromatoporoid skeletons unidentifiable. This situation is particularly true for fauna within the stromatoporoid biostromal facies at Kirkland Downs area where neomorphism and dolomitisation have rendered

TABLE 7. Major faunal components of the *Gerronostroma hendersoni- Hermatostroma maculatum* community and their guild memberships, with dominant forms in bold.

Constructors	Encrusters (Pavers)	Bafflers	Dwellers
Gerronostroma hendersoni	Clathrocoilona abeona	**Stachyodes costulata**	**Heliolites sp.**
Hermatostroma maculatum	Euryamphipora merlini	Thamnopora s .	Alveolites sp.
Actinostroma filitextum	Aulopora sp.	Cladopora sp.	numerous rugose corals
Atelodictyon fallax	Alveolites sp.	Stringophyllum spp.	Litophyllum koninckii
Stromatopora huepschii	(Gerronostroma hendersoni)	Alveolites sp.	brachiopods
Salairella bucheliensis	(Hermatostroma maculatum)	Gen. et sp. indet cf.	molluscs
Coenostroma wyatti		Clathrodictyella	Romingeria sp.
Anostylostroma ponderosum			Syringopora sp.
Parallelopora? sp.			
Clathrodictyon sp.			

TABLE 8. Faunal components of the *Coenostroma- Hermatostroma episcopale* community and their guild designations, with dominant components in bold.

Pavers	Encrusters	Bafflers	Dwellers
Hermatostroma episcopale	*Aulopora* sp.	*Amphipora pervesiculata*	*Heliolites* sp.
Coenostroma burdekinense	*Alveolites* sp.	*Cladopora* sp.	atrypids
Coenostroma wyatti	*Clathrocoilona abeona*	*Alveolites* sp.	other brachiopods
Salairella bucheliensis	*Euryamphipora merlini*	*Aphyllum* sp.	*Syringopora* sp.
Stromatopora huepschii		*Stringophyllum* sp.	molluscs
Glyptostromoides boiarschinovi		*Stachyodes costulata*	*Romingeria* sp.
Stromatopora sp.		*Stachyodes* sp. A	other rugose corals
Parallelopora sp.		*Stachyodes* sp. B	
Salairella sp.			
Stictostroma sp.			
Aculatostroma sp.			
Litophyllum koninckii			

most stromatoporoids unidentifiable to species level. Present at this locality are the stromatoporoids; *Amphipora ramosa, Stromatopora* cf. *S. huepschii* (with caunopores), *Hermatostroma* cf. *H. maculatum, H. episcopale, Stromatopora* sp. and a number of unidentifiable taxa; tabulate corals *Heliolites* sp., *Syringopora* sp., large *Alveolites* sp., fasciculate *Alveolites* sp., *Cladopora* sp. and the chaetetid *Litophyllum koninckii*. Additionally there are a large number of colonial rugose corals, particularly *Taimyrophyllum* spp. (Zhen, 1991). The biostromal fauna at Kirkland Downs is tentatively assigned to this community.

GERRONOSTROMA HENDERSONI-HERMATOSTROMA MACULATUM COMMUNITY (Table 7). This community was the main reef-occupying faunal assemblage. It is found within patch reefs of the nodular limestone facies, laminar stromatoporoid pavements of the coverstone facies, and the biohermal complex including primary reefal framestone and grainy floatstone representing inter-reef channel. The 2 constructors are *G. hendersoni* and *H. maculatum*. There are no non-stromatoporoid constructor guild members within the reefal complex. Large tabulate corals are a subsidiary component of the reefal community, and do not form part of the essential reefal framework. There is moderate diversity in the baffler and dweller guilds, with an abundant rugose coral and fasciculate tabulate coral fauna. Guild overlap is

demonstrated by the main elements of the fauna. Within the laminar stromatoporoid pavement *G. hendersoni, H. maculatum,* and less commonly *Parallelopora*? sp. should be regarded as paver guild members.

This community was restricted seaward by depth, and leeward by siliciclastics, represented either by moderate input of fine siliciclastics or by coarse siliciclastic mobile substrates. The community could survive within the muddy carbonate lagoon where substrate was available and when sedimentation rate permitted.

COENOSTROMA-HERMATOSTROMA EPISCOPALE COMMUNITY (Table 8). This community is found within the dispersed stromatoporoid pavements and coral thickets of the dispersed stromatoporoid packstone facies, overlapping to the coralline packstone facies best characterised by the *Amphipora pervesiculata* community described below. It is dominated by baffler guild members, with a significant representatives of paver guild members. It is restricted seaward by depth, and landward by the biostromal and biohermal zones. Given that some elements of this fauna are found in the biohermal and biostromal facies as part of other

TABLE 9. Faunal components of the *Amphipora pervesiculata* community and their interpreted guild memberships, with dominant taxa in bold.

Pavers	Encrusters	Bafflers	Dwellers
Hermatostroma episcopale	*Aulopora* sp.	**Amphipora pervesiculata**	brachiopods
Salairella bucheliensis	*Alveolites* sp.	**Cladopora sp.**	molluscs
Stromatopora huepschii	*Syringopora* sp.	**Alveolites sp.**	rugose corals
Coenostroma burdekinense	*Euryamphipora merlini*	*Aphyllum* sp.	*Syringopora* sp.
Coenostroma wyatti		*Stringophyllum* sp.	gastropods
Heliolites sp.		rare *Stachyodes* spp.	

communities, it appears that they could not compete effectively with other taxa in such communities. Sedimentation rate was probably too high in the biohermal and biostromal facies with siliciclastic input at the limits of tolerance for the main elements of the *Coenostroma-Hermatostroma episcopale* community.

AMPHIPORA PERVESICULATA COMMUNITY (Table 9). Delicate *Amphipora* dominated this community, living within thickets of the coralline packstone and dispersed stromatoporoid packstone facies. Larger skeletal members of the community, particularly stromatoporoids and heliolitids, are minor faunal components. There is a high proportion of thinly branched stromatoporoids, tabulate corals and long-branched rugose corals. The community extended from the seaward edge of the bioherm and biostromal complex, well across the shallow distal shelf. Where there was limited biohermal or biostromal development, the community extended across the entire carbonate-dominant shallow shelf. *Amphipora* has been traditionally regarded as a lagoonal faunal component (Noble, 1970), however, the presence of *A. pervesiculata* in a number of different, if adjacent, facies, suggests that the genus may have been more widely distibuted through the available niches. Toppling and reorientation of the many delicately branched skeletons suggest an ambient environment with gentle current activity.

Isolated colonies of *Syringopora* sp and *Aulopora* sp. are common to the community. These are regarded as 'pioneers', often inhabiting substrates and areas seemingly unsuited to other groups.

ENDOPHYLLUM COMMUNITY (Table 10). This community is restricted to the *Endophyllum* siltstone facies, and is dominated by the large colonial rugose coral. The role of stromatoporoids is much reduced in this community where they are restricted to the encruster guild, subordinate to tabulate and rugose corals and the chaetetid *Litophyllum koninckii*. Bafflers are dominated by dendroid tabulate corals, possibly inherited from the vertically (and hence laterally adjacent) coralline packstone facies.

TABLE 10. Members of the *Endophyllum* community and their guild designations with dominant forms in bold.

Constructors	Encrusters	Bafflers	Dwellers
Endophyllum sp.	*Clathrocoilona spissa*	*Alveolites* sp.	atrypids
rare sponges	*Stromatopora huepschii*	*Cladopora* sp.	other brachiopods
larger alveolitids	*Salairella bucheliensis*	*Dohmophyllum* sp.	other rugose corals
Heliolites sp.	*Aulopora* sp.	*Stringophyllum* sp.	
Litophyllum koninckii	*Alveolites* sp.		
Alveolites sp.	*Litophyllum koninckii*		

CEPHALOPOD ASSOCIATION. This 'association' occupies the micritic carbonate facies, in the deeper shelf zone. It is a depauperate fauna consisting of scattered nautiloids, including *Diademoceras* rare atrypids, particularly *Desquamatia* sp., and rare ramose alveolitid fragments, tentatively assigned to *Cladopora* sp. The association represents a mixing of nektonic cephalopods and benthic forms which sporadically grew on the sea floor at the limits of the photic zone.

BIOGEOGRAPHIC RELATIONSHIPS

Blodgett, Rohr, & Boucot (1990) remarked that the poorly known Givetian gastropods from Australia indicate a high degree of endemism, but this was based on only the study of Heidecker (1959). Work subsequent to 1990 has demonstrated that whilst this comment is essentially true, there are some affinities with Old World faunas. The bivalve *Tanaodon louderbacki* was first described from Sichuan and is also known from Guangxi, China (Kirk, 1927; Pojeta, 1986). Modiomorphs are common elements to both Old World and Eastern Americas Realms, during the Givetian. Indeed *Phenacocyclas* suggests Eastern Americas realm affinities. Of the gastropods *Burdikinia, Austerum* are known only from the adjacent Broken River Province, but *Labrocuspis* has been reported from the Kitikami Mountains in Japan (Kase, 1989). Preliminary observations of small collections the smaller gastropod fauna from the other parts of the Burdekin Formation suggests high numbers of murchisoniids, which suggest old world Givetian affinities (Blodgett, Rohr & Boucot, 1990).

The Givetian was a time of maximum cosmopolitanism for stromatoporoids, more so than for brachiopods and rugose corals (Stock 1990). At a generic level, the Burdekin stromatoporoid fauna shows strong affinities with faunas of the Old World Realm rich in

FIG. 17. Palaeobiogeographic affinities of the Burdekin stromatoporoid fauna showing the distribution of species found within the Burdekin fauna with numbers indicating the number of species common to both Burdekin and other localities. Reconstruction and localities follow Stock (1990) and McKerrow & Scotese (1990) for the Givetian time.

amphiporids, clathrodictyids, stromatoporids and syringostromellids.

Generic level affinities of the fauna are difficult to assess given its cosmopolitan nature. Based on the material confidently assigned to species, greatest affinities are with faunas from Guangxi, Poland, and Belgium but elements of the fauna are known from many other, mostly Old World, faunas (Fig. 17). There is considerable affinity with Givetian to Frasnian faunas worldwide.

Comparison with the adjacent Broken River Province is difficult given the limited studies of Mallett (1968, et seq.). Re-examination of Mallett's collections and additional material from the Broken River area is being undertaken by Webby & Zhen (pers. comm.) and has been published in part (Webby & Zhen 1997) who recognise modest numbers of *Salairella* species within the Middle Devonian assemblage. Examination of spot collections and the material of Mallett (1968) indicates that there are some similarities with the Burdekin fauna but proper evaluation must await completion of the work being undertaken by Webby and Zhen.

Preliminary assessment of Broken River spot collections is as follows:

Spanner Limestone Member Papilio Formation, Givetian (*varcus* zone)

Taxa present: *Stromatopora huepschii*
Coenostroma sp.
Salairella buecheliensis
Salairella sp.
Actinostroma sp.
Clathrocoilona sp.

Stanley Limestone member of the Mytton Formation-Late Givetian (*disparilis* zone)
Stromatopora huepschii
Salairella buecheliensis
Salairella sp.
Actinostroma sp.
Hermatostroma sp. cf. *H. schluteri*
Hermatostroma sp. cf *H. epsicopale*
Clathrocoilona sp. cf. *Clathrocoilona solida*
Stachyodes sp.
Dosey Limestone, Eifelian to Givetian
Stromatopora huepschii
Salairella sp.
?*Actinostroma* sp.
?*Trupetostroma* sp.
Gerronostroma sp.
Salairella sp. cf. *S. cooperi.*

Mallett (1968) recorded a large number of taxa from the 'Couvinian' to Givetian Dip Ck and Chinamans Ck Limestones, but only a few of these were ever published (Mallett, 1970a,b; 1971). Unpublished taxa include a number of species of *Stromatopora* including *S. huepschii,*
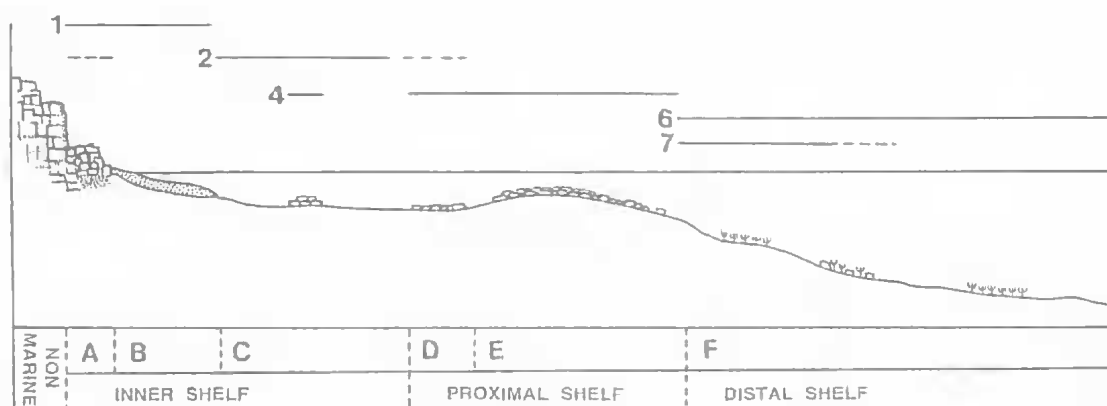
FIG. 18. Shelfal sedimentary assemblages and community distribution for deposition of the Big Bend Arkose and Burdekin Formation for the Fletcherview-Burdekin Downs area. 1, *Burdikinia* community; 2. *Stachyodes-Syringopora* community; 3, *Clathrocoilona spissa-Aulopora* community; 4, *Gerronostroma hendersoni-Hermatostroma maculatum* community; 5, *Ferestromatopora heideckeri-Amphipora-Stringocephalus* community; 6, *Amphipora pervesiculata* community. 7, *Hermatostroma episcopale- Coenostroma* community; 8, cephalopod association. A, abraded fossil, coarse siliciclastic facies; B, fossiliferous sandstone facies and impure limestone/ sandstone facies; C, nodular limestone facies; D, coverstone subfacies; E, facies of the biohermal complex; F, coralline packstone facies.

A. ramosa (also mentioned by Jell, 1967), *Stromatopora (Ferestromatopora) tyrganensis* Yavorksy, *Gerronostroma 'concentricum'*, a number of species of *Hermatostroma*, *Stictostroma*, *Anostylostroma* and *Actinostroma*. Brief examination of collections from this unit confirms the presence of *Salairella*, *Stromatoporella*, *Atelodictyon* and *Trupetostroma*. Mallett (1968, 1970a,b, 1971) recorded a number of *Actinostroma* species, most of which remain unpublished, within the Dip Ck and Chinamans Ck Limestone compared with the single species known from the Fanning River Group.

Webby & Zhen (1997) have recently published some of their taxonomic work based on Mallett's and additional materials. They record are *Actinostroma clathratum* Nicholson, *Aculatostroma* sp. *Nexililamina dipcreekensis* Mallett, *Hermatostroma malleti* Webby & Zhen, *Trupetostroma? tubulosum* (Mallett) and *Amnestostroma steloges* (Mallett) from the upper Eifelian to ?lower Givetian Dip Ck Limestone; *Actinostroma clathratum* Nicholson and *Hermatostroma malleti* Webby & Zhen from the upper part of the Chinaman Ck Limestone (early Givetian), and *Gerronostroma* sp. and *Stachyodes costulata* Lecompte from the Stanley Limestone Member of the Mytton Formation which is latest Givetian in age. From this it is clear that there are some specific differences and commonalities between the Burdekin and Broken River faunas, as would be expected Perhaps differences could be accounted for by the difference palaeogeographic settings and the slight age differences between the described taxa The Broken River carbonate platforms were more open marine conditions in comparison to the resticted embayed nature of the Burdekin Basin.

Zhen (1991) discussed the affinities of the abundant rugose coral fauna of the Fanning River Group. He recognised significant similarities with late Early to Middle Devonian faunas from Germany, southwest China, northwest China, south China and the Urals, and recognised other affinitites with central Asia, Vietnam and North America. Zhen (1991) also noted similarities with New South Wales and north Queensland rugose coral faunas, but assessment of the relationships of these faunas awaits systematic assessment of their stromatoporoids.

CONCLUSIONS

Ten faunal communities are recognised based on the study and distribution of stromatoporoid and selected molluscan taxa, and the distribution of tabulate and rugose corals. These communities vary according to the 2 styles of shelf assemblage. The specific relationships between the facies of Cook (1995) and the communities here presented is given in Figs 18 and 19. The *Burdikinia* community is a robust gastropod-
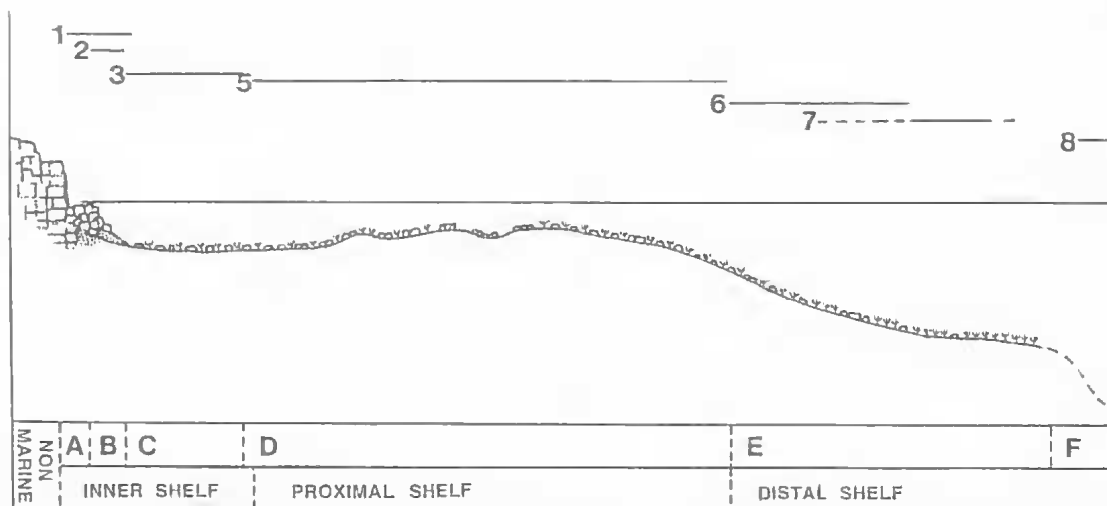
FIG. 19. Shelfal sedimentary assemblages and community distribution for deposition of Big Bend Arkose and Burdekin Formation for deposition of the Big Bend Arkose and Burdekin Formation for the Fanning River area. 1. *Burdikinia* community; 2, *Stachyodes-Syringopora* community; 3, *Clathrocoilona spissa-Aulopora* community; 4, *Gerronostroma hendersoni-Hermatostroma maculatum* community; 5, *Ferestromatopora heideckeri-Amphipora-Stringocephalus* community; 6, *Amphipora pervesiculata* community; 7, *Hermatostroma episcopale-Coenostroma* community; 8, cephalopod association.

A, abraded fossil, coarse siliciclastic facies; B, fossiliferous sandstone facies; C, fossiliferous siltstone and innermost silty biostromal facies group; D, facies of the biostromal complex; E, coralline packstone facies; F, micritic carbonate facies.

dominant community which occupies the coarse siliciclastic inner shelf, and the *Modiomorpha* community occurs as a rare but distinctive in situ shell bed. The *Stachyodes costulata-Syringopora* community occurs within inner shelf muddy impure carbonate lagoons, but elements were able to inhabit interstitial niches in subtidal marine headlands. In the Fletcherview-Burdekin Downs area, the *Hermatostroma maculatum-Gerronostroma hendersoni* community inhabited patch reefs in the inner shelf, backreef laminar stromatoporoid pavements and the main reefal environments. The *Clathrocoilona spissa-Aulopora* community occupied nearshore, fringing biostromes in the Fanning River area. The *Ferestromatopora heideckeri-Amphipora ramosa-Stringocephalus* community occupied extensive nearshore to offshore biostromes within the Fanning River-Golden Valley areas whereas the *Coenostroma-Hermatostroma episcopale* community dwelt within dispersed stromatoporoid pavements and, more sparsely, within offshore coralline thickets. The *Amphipora pervesiculata* community dominated dendroid stromatoporoid-coralline thickets adjacent to and seaward of bioherms, dispersed stromatoporoid pavements and

stromatoporoid biostromes particularly in the Fletcherview-Burdekin Downs area. The *Endophyllum* community was restricted to patch reefs which grew during regressive phase, carbonate to siliciclastic transition. The cephalopod association is represented by a sparse fauna found within deeper water, micritic carbonate facies in the Golden valley area.

Within the Kirkland Downs area, poor preservation prevents accurate assessment of the stromatoporoid fauna, but biostromal deposits are dominated by colonial rugose corals, in addition to elements probably related to the *Ferestromatopora-Amphipora ramosa-Stringocephalus* community.

Stromatoporoid shape is controlled by both ecologic and genetic factors. Interactions of sedimentation rate, substrate type and availability, depositional energy and siliciclastic input demonstrably influence shape. Many stromatoporoid taxa display shape ranges rather than restricted gross morphologies.

The distribution of taxa indicates that most stromatoporoids occupied a range of environments on the shallow shelf, but some, such as *Amphipora ramosa*, were more restricted in their distribution.
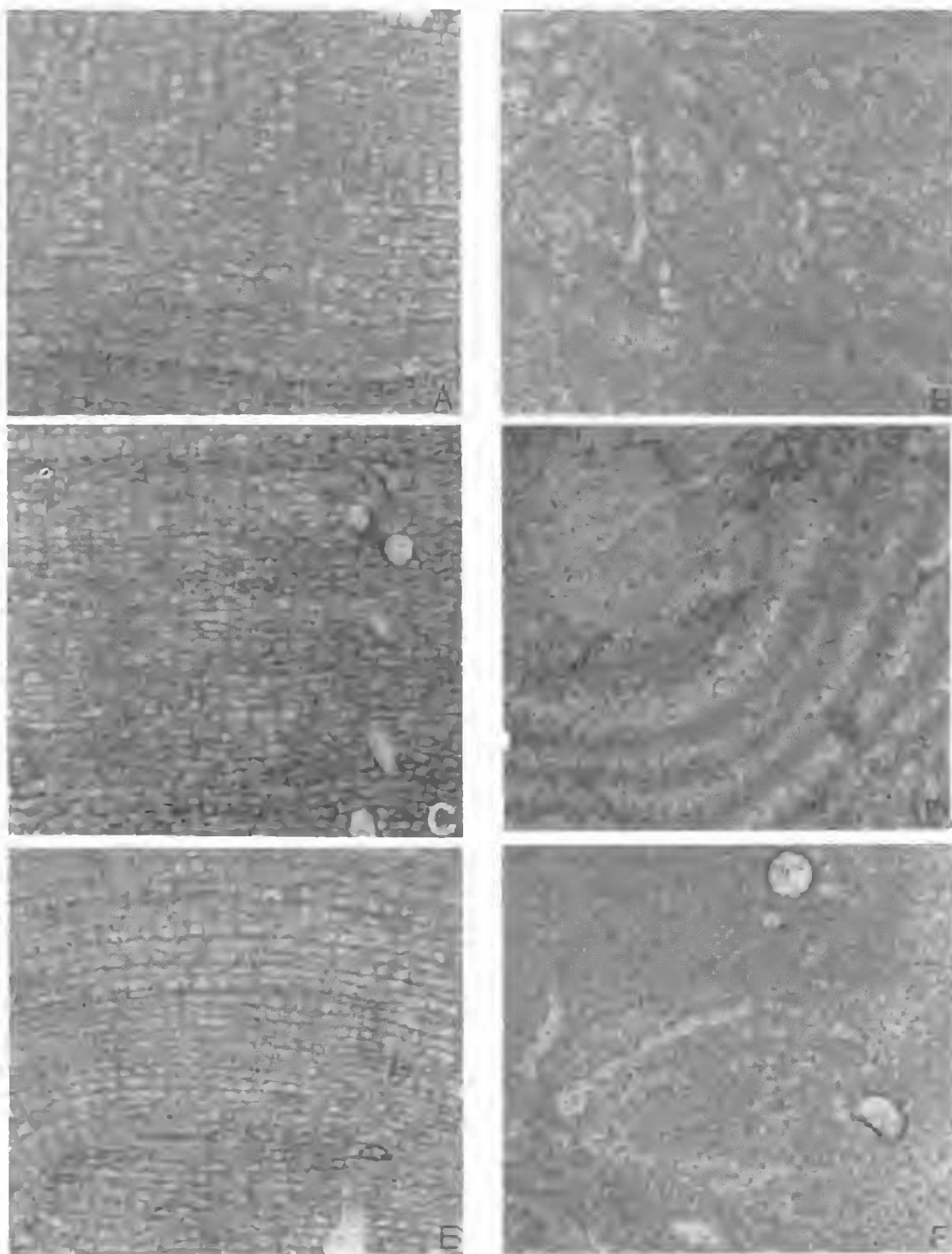
FIG. 20. *Actinostroma filitextum* Lecompte, 1951. A, B, JCUF11935 × 10. Section. C, D, JCUF11939 × 10. E, F, JCUF11879 × 10. A, C, E, vertical section. B, D, F, tangential section.
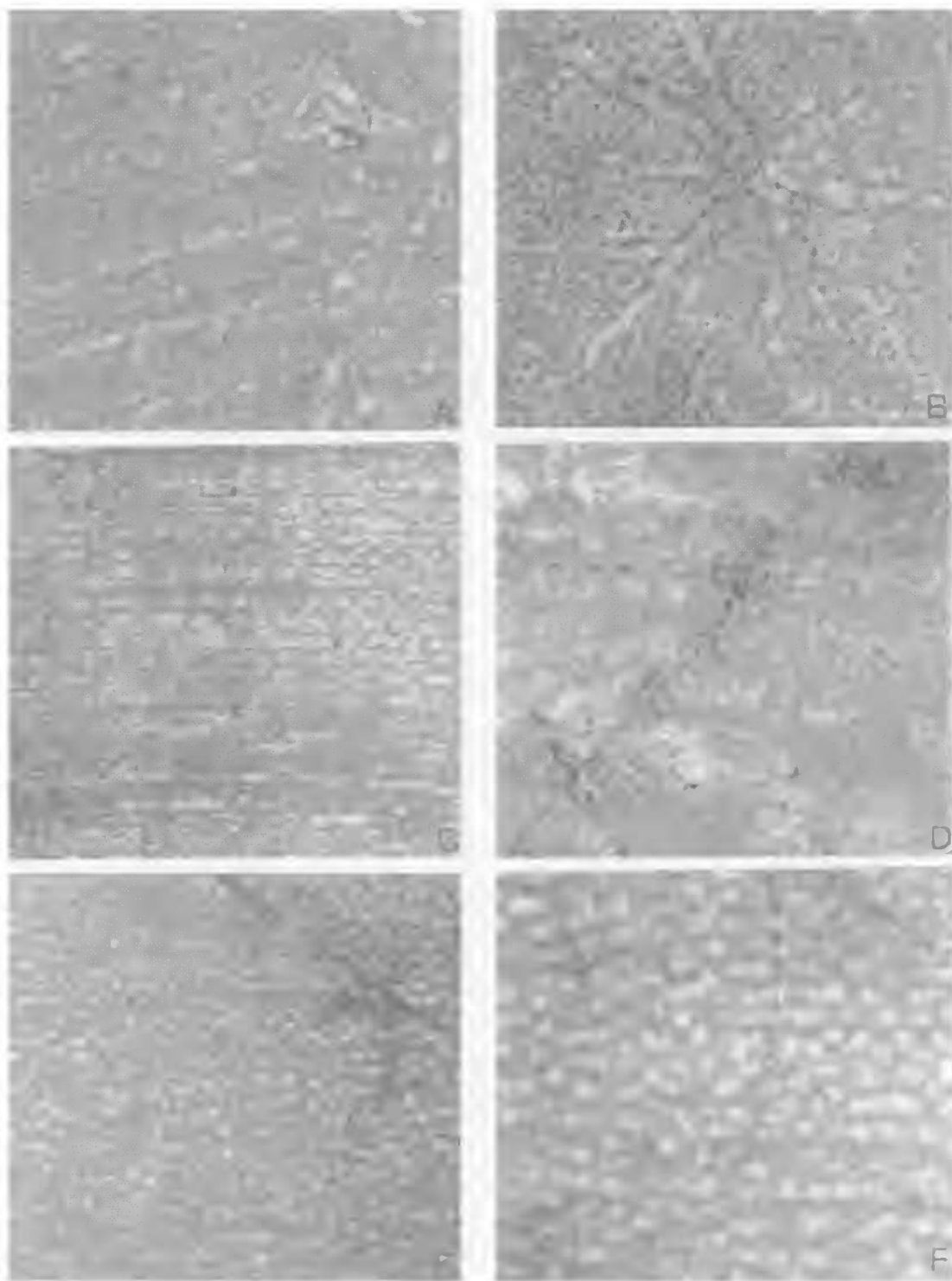
FIG. 21. A, B, *Actinostroma filitextum* Lecompte, 1951. JCUF11881 × 10. A, vertical section; B, tangential section. C,D, *Aculatostroma* sp. JCUF11942 × 10. C, vertical section; D, tangential section. E, F, *Clathrodictyon* sp. JCUF12004. E, vertical section × 10; F, vertical section × 20.

Overgrowth phenomena occur within most depositional environments of the Burdekin Formation, but particularly complex and common overgrowths were found within nearshore, siliciclastic-dominant biostromal units at Fanning River. This situation is interpreted to represent preservation of the organisms from a biostrome that had been stressed by the effects of nearshore siliciclastic sedimentary processes.

Stromatoporoid intergrowths are common within the fauna, particularly those involving *?Syringoporella* sp, which is associated with stromatoporoids with more irregular skeletal architecture. Distribution of *?Syringoporella* sp. is regular, and skeletal response by their host stromatoporoids is evident. The absence of micritic envelopes on tabulate walls suggests that the coral growth surface matched that of the stromatoporoid host. Other intergrowths include sporadic *Syringopora*? sp., a number of rugose corals and symbionts allied to *Helicosalpinx* sp.

Designation of guild membership within communities has required adaptation of the reefal guild structure concept of Fagerstrom (1987) to allow for non-reefal, biostromal communities. Some taxa demonstrated guild overlap between facies.

Taxonomic analysis of the fauna has determined the presence of 35 stromatoporoid taxa, of which 6 are previously undescribed. Fourteen species are left in open nomenclature.

Bivalves and gastropods show Old World Realm affinites and the stromatoporoid fauna shows strongest affinities with Early to Middle Devonian faunas in China, Europe, Germany, France and Late Devonian reefal faunas in Western Australia.

SYSTEMATIC PALAEONTOLOGY

PORIFERA Grant, 1836
STROMATOPOROIDEA
Nicholson & Murie, 1878
ACTINOSTROMATIDA
Bogoyavlenskaya, 1969
ACTINOSTROMATIDAE
Nicholson, 1886b

Actinostroma Nicholson, 1886b

Actinostroma Nicholson, 1886b: 75; Lecompte 1951: 67; Galloway & St. Jean 1957: 148; Galloway 1957: 437; Stearn 1966a: 86; Flügel & Flügel-Kahler 1968: 522; Kazmierczak 1971: 129; Zukalová 1971; Mallett 1971: 235; Yang & Dong 1979: 30; Stearn 1980: 888; Stock 1982: 669; Stock 1984: 774; Bogoyavlenskaya & Khromych 1985: 66.
?Trigonostroma Bogoyavlenskaya 1969: 463 (transl.).
Bullatella Bogoyavlenskaya 1977b: 13.
Auroriina Bogoyavlenskaya 1977b: 16.
Lamellistroma Bogoyavlenskaya 1977b: 17.

TYPE SPECIES. *A. clathratum* Nicholson, 1886a by original designation from Gerolstein, Middle Devonian of Germany.

DISTRIBUTION AND AGE. Silurian to Late Devonian (Frasnian), widespread in Old World Realm and found in Eastern Americs Realm from the Givetian (Flügel & Flügel-Kahler, 1968; Stearn, 1979; Cockbain, 1989).

REMARKS. Identification of the hexactinellid network is critical to the definition of the genus. Although it is variably developed and preserved (Stearn, 1966; Mistiaen, 1985), most authors regard it as a fundamental character. Sleumer (1969) argued for a much wider concept of the genus to include non-hexactinellid forms like *Gerronostroma* Yavorksy. Although variable preservation of the network is evident in Burdekin material, even within single slides, the network is regarded as a vital generic character, and Sleumer's (1969) wide generic concept is hence rejected.

Flügel & Flügel-Kahler (1968) recorded over 100 species for the genus, and Bogoyavlenskaya & Khromych (1985) recorded an additional 5 taxa. New species assigned to *Actinostroma* by Chinese authors include 3 described by Yang & Dong (1979) and 5 from Dong, Wang & Fu (1989). Cockbain (1984) has contributed one new species from the Canning Basin, W.A. The large number of species of this genus is testament not only to its wide spatial and temporal distribution, but also to the reluctance of some authors to 'lump'. Most taxa of *Actinostroma* have been differentiated on the basis of laminae and pillar spacings (see Lecompte, 1951; Flügel, 1959; Mallett, 1971). Use of 'art-feld' diagrams (Flügel, 1959) and gallery indices (Klovan, 1966; Mallett, 1971; Cockbain, 1984) have further quantified characters differentiating species. Strict use of statistical tools for the differentiation of stromatoporoid taxa must take account of the high degree of variation (Cockbain, 1979; Stearn, 1989). Stearn (1989) argued that the species concept in stromatoporoids is generally too narrow and that the use of average measured skeletal parameters will not be useful in species determination unless the measured structures are homologous. However, most authors do not
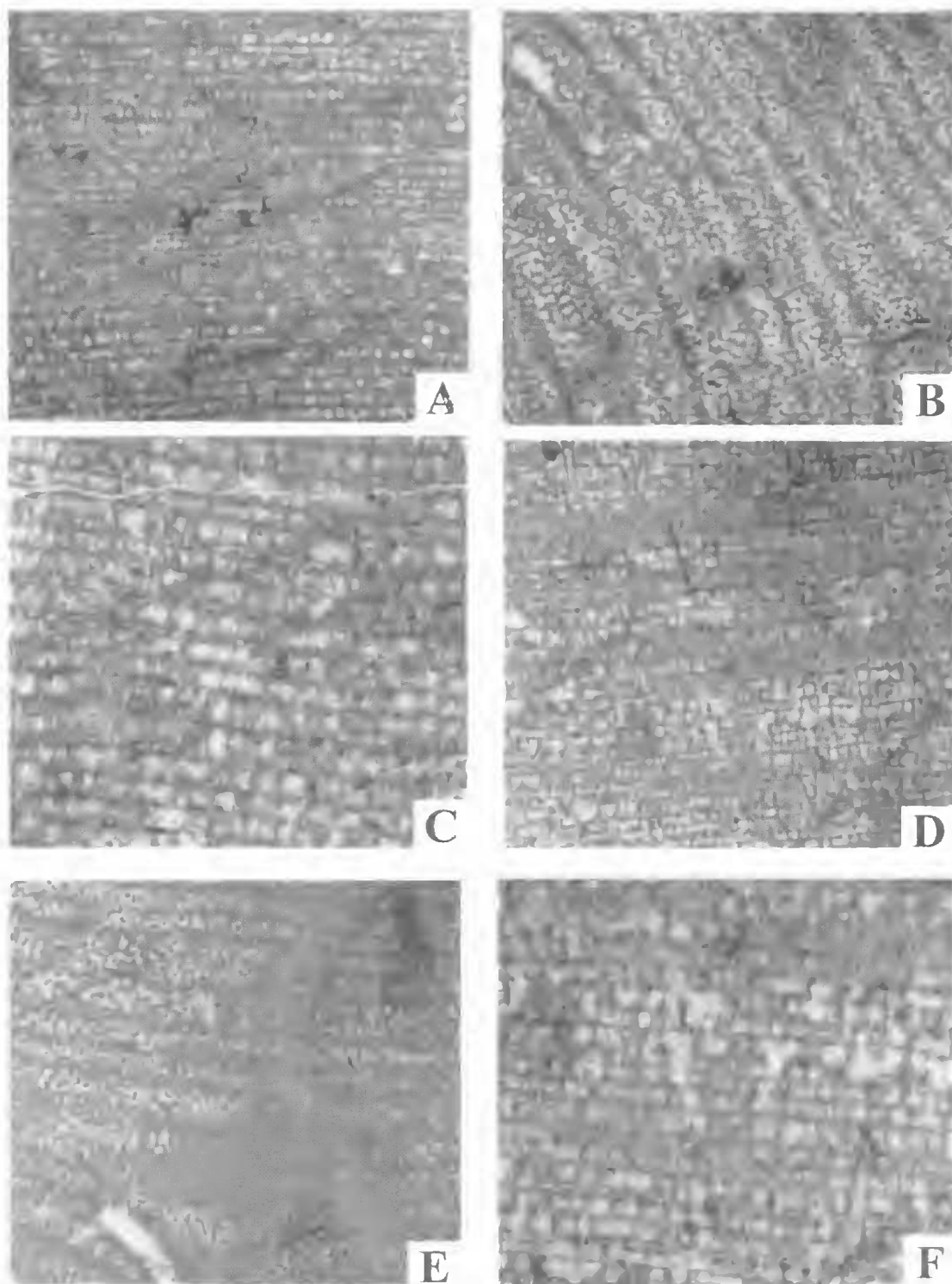
FIG. 22. *Atelodictyon fallax* Lecompte, 1951. A-C, JCUF11882. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D-F, JCUF11883. D, vertical section × 10; E, tangential section × 10; F, vertical section × 20.

detail how measured skeletal parameters were derived; it can only be assumed that measurements are from similar parts of the skeleton. Cockbain (1984) used pillar and laminar spacings and a gallery index (a reciprocal of Klovan's 1966 index) to synonymise *A. papillosum* (Bargatzky), *A. clathratum* Nicholson, *A. subclathratum* Etheridge Jr and *A devonense* Lecompte allowing for a wide species concept. Mistiaen (1985) disagreed with this synonymy maintaining *A. clathratum*, *A. papillosum* and *A. devonense* as distinct taxa. Webby & Zhen (1993) questioned the status of *A. papillosum* given its inadequate illustration. Relationships among these taxa will be a matter of continued debate.

This work adopts a wide species concept for *A. filitextum* Lecompte, allowing for a range of morphometric values. *A. filitextum* Lecompte, *A reversum* Lecompte and probably *A. perlaminatum* Lecompte are considered to be synonymous, representing a gradation through delicately constructed actinostromid morphology.

Stearn (1980) has discussed the synonymy of *Trigonostroma* Bogoyavlenskaya 1969, *Bullatella* Bogoyavlenskaya 1977b, *Auroriina* Bogoyavlenskaya 1977b and *Lamellistroma* Bogoyavlenskaya 1977b. Bogoyavlenskaya & Khromych (1985) record no further use of these genera beyond their original descriptions. Webby (pers. comm.) has kindly pointed out that *Trigonostroma* is possibly a coral, and hence is a highly doubtful synonym.

Actinostroma filitextum Lecompte 1951
(Figs 20, 21A,B.)

?1951 *Actinostroma perlaminatum* Lecompte: 120, pl. 12, fig. 4; Mistiaen: 48, pl. 2, figs. 4-5.
1951 *Actinostroma filitextum* Lecompte: 121 pl 13, fig. 1; Mistiaen 1985:46, pl. 1, figs. 8-10, pl. 2, fig. 6.
1951 *Actinostroma reversum* Lecompte: 121 pl.13, fig. 2.
?1963 *Actinostroma* cf. *filitextum* Lecompte: Yang & Dong: 152 (170 trans.), pl. 4, figs. 5-6.

MATERIAL. JCUF11877-81, 11935-7, ?11939-41, 11842, from JCUL778, JCUF11934 from float near JCUL778, JCUF11942-3 from JCUL787.

DESCRIPTION. Form apparently medium domical, known from only fragments up to 100mm high and 160mm wide. Skeleton with variably spaced latilaminae. Thick (0.04-0.10mm), continuous pillars which intersect many laminae spaced 16-26 per 5mm (mean = 21.3, σ=2.2) joined in a hexactinellid network or rounded in cross-section. Laminae composed of

joined colliculi, typically gently undulating, uncommonly strongly undulose, and variably discontinuous; thinner than pillars; (0.03-0.05mm thick) spaced 27-37 per 5mm (mean = 30.2, σ=2.1). Hexactinellid network moderately-well developed. Astrohizae present, 5-8mm apart, stellate, with distal dichotomous branching of longer canals. Skeletal material compact.

MORPHOMETRICS. This and subsequent tables present data as mean (σ = standard deviation), N=10 unless otherwise specified, P5= pillars per 5mm, Pt= pillar thickness, L5, laminae per 5mm, Lt= laminar thickness.

Specimen	P5	Pt	L5	Lt
JCUF11877	22.8 (1.9)	0.09 (0.02)	31.4 (1.8)	0.04 (0.02)
JCUF11878	20.2 (2.2)	0.04 (0.02)	28.4 (1.8)	0.03 (0.01)
JCUF11879	21.8 (2.4)	0.09 (0.01)	28.8 (2.6)	0.05 (0.01)
JCUF11880	21.4 (2.2)	0.09 (0.03)	32.1 (2.3)	0.04 (0.01)
Average	21.6 (2.2)	0.08 (0.02)	30.2 (2.1)	0.04 (0.01)

DISTRIBUTION AND AGE. Burdekin Basin, north Queensland, Australia, Givetian; ?Gueizhou, China, Eifelian; Dinant Basin, Belgium, ?Givetian and Frasnian; Afghanistan, Late Devonian.

REMARKS. The characteristic continuous pillars and obvious hexactinellid network confirm the Burdekin material as *Actinostroma*. The large range of pillar and collicular spacings demonstrates the high degree of variation within the specimens, given that all data came from the middle of skeletons. The material is characteristic of the delicate architecture of *A. filitextum* Lecompte and is assigned to that species. *A. crassepilatum* Lecompte and *A. reversum* were differentiated from *A. filtiextum* by collicular spacing, the thicker pillars, and astrorhizal characteristics (Lecompte, 1951: 121) although the latter must be regarded as a dubious for separation. Whilst *A. crassepilatum* has markedly thicker pillars, *A. reversum* has pillars only a little thicker. *A. perlaminatum* has very closely spaced pillars and laminae, and may represent an extreme morphotype; a tentative synonymy is suggested.

Aculatostroma Khalfina, 1968

TYPE SPECIES. *Syringostroma verrucosum* Khalfina, 1961 from the Lower Devonian, Salair, Siberia, by subsequent designation.
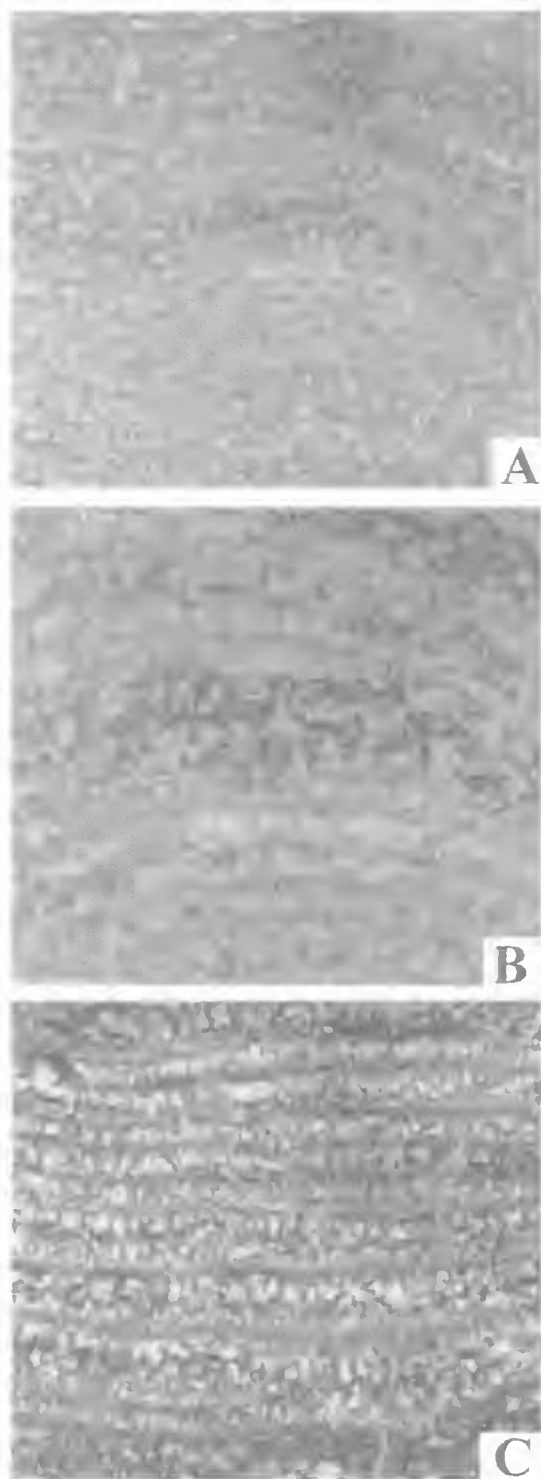
FIG. 23. *Schistodictyon* sp. JCUF12014. A, vertical section × 10; B, vertical section × 20; C, oblique tangential section × 10.

REMARKS. Stearn (1991) has provided a synonymy and a full discussion of the genus. Webby, Stearn & Zhen (1993) recorded a doubtful taxon from the Lower Devonian of Victoria.

Aculatostroma? sp.
(Fig. 21C,D)

MATERIAL. JCUF11942-3 from JCUL787.

DESCRIPTION. Two fragmental specimens from laminar skeletons; laminae dominant, straight to very gently undulose, generally persistent; approximately 10-11 per 2mm, variable in thickness, but thin (0.02-0.05mm). Pillars slightly thicker, 0.02-0.08mm, very irregularly spaced so that measurement is difficult. Pillars commonly branch in interlaminar space or flare upwards to form colliculate laminae. Both laminae and pillars are composed of compact skeletal material. Dissepiments common in irregular, horizontally elongate galleries. In tangential section the skeletal elements are poorly preserved. Short pillar chains are evident, and pillars are rarely isolated. Simple walled astrorhizae are present.

REMARKS. The upward flaring of pillars to form colliculate, but persistent, laminae suggests assignment to *Aculatostroma* Khalfina. The poor preservation of tangential section and the relative persistence of laminae leaves the generic assignment open to question.

CLATHRODICTYIDA
Bogoyavlenskaya, 1969
CLATHRODICTYIDAE Kühn, 1939
Clathrodictyon Nicholson & Murie, 1878

Clathrodictyon Nicholson & Murie 1878: 220; Flügel & Flügel-Kahler 1968: 534; Bogoyavlenskaya & Khromych 1985: 72; Stearn 1991: 617.

TYPE SPECIES. *Clathrodictyon vesiculosum* Nicholson & Murie, 1878 from the Early Silurian of Ohio, U.S.A. by original designation.

DISTRIBUTION AND AGE. Worldwide, Ordovician to Late Devonian.

REMARKS. A recent review and synonymy of the genus was provided by Stearn (1991) and Flügel & Flügel-Kahler (1968) provided an earlier, comprehensive synonymy.

Clathrodictyon sp.
(Fig. 21E,F)

MATERIAL. JCUF12004, single specimen from JCUL782.

DESCRIPTION. Single fragment from a low domical skeleton greater than 2cm thick and 5cm wide. In vertical section laminae long, compact and downwardly inflected to form pillars, with a gentle chevroned appearance, spaced approximately 9-11 per 2mm, of variable thickness (0.02-0.08mm). Pillars short, not superposed, formed by inflections of laminae, spaced approximately 7-10 per 2mm, generally slightly thicker (0.02-0.10mm) than laminae. Galleries horizontally elongate, somewhat lenticular, or rounded. No dissepiments or astrorhizal traces were seen. Skeletal material compact.

REMARKS. Characteristic inflection of laminae to produce pillars, and the lenticular galleries are characteristic of *Clathrodictyon*. Assignment of species affinities requires more extensive material.

Atelodictyon Lecompte 1951

Atelodictyon Lecompte 1951: 124; Flügel & Flügel-Kahler 1968: 529; Fischbuch 1969: 169; Zukalová 1971: 40; Khromych 1974: 31; Stearn 1975b: 1646; Khromych 1976: 46; Mistiaen 1980: 188; Bogoyavlenskaya & Khromych 1985: 69; Stearn 1991: 618.
Not *Atelodictyon* Lecompte, Galloway & St Jean 1957: 122; Galloway 1957: 435; Stearn 1966a: 87; Kazmierczak 1971: 127; Stearn 1980: 894; Stock 1982: 661; Mistiaen 1985: 54.

TYPE SPECIES. *Atelodictyon fallax* Lecompte, 1951 from the Middle Devonian of Belgium by original designation.

DISTRIBUTION AND AGE. Worldwide, Early to Late Devonian.

REMARKS. Stearn (1991) has discussed the particular problems of this genus. In addition to the taxa listed by Stearn (1991) as belonging in *Atelodictyon*, *A. dewalense* Mistiaen, 1985 appears to be a valid designation. *A. connectum* Yang & Dong, 1979 (Plate 4, fig 7,8) shows somewhat discontinuous laminae and is probably not *Atelodictyon*.

Atelodictyon fallax Lecompte 1951
(Fig. 22)

Atelodictyon fallax Lecompte 1951: 125, pl. 15, figs 1a-d; Galloway & St. Jean 1957: 122, pl. 6; Flügel & Flügel-Kahler 1968: 156; Fischbuch 1969: 169, pl.1, figs 1-5; Yang & Dong 1979: 22, pl. 4, figs.1-4; Dong et al. ?1989: 265, pl. 7, figs. 1a,b.

MATERIAL. JCUF11882-84, 11886-89, 12003 all from Fanning River type section JCUL788.

DESCRIPTION. Skeleton medium domical, latilaminate. Laminae continuous, gently undulose spaced 20-26 per 5mm (mean =24, n= 10), relatively thin (0.08-0.12mm). Pillars 25-35 (mean = 30.8, n=10) per 5mm, thin (0.08-0.16mm) commonly superposed or complex in vertical section, forming chain-like network in tangential section. Astrorhizal canals common, sporadically crossed by dissepiments. Skeletal material compact.

DISTRIBUTION AND AGE. Burdckin Basin, North Queensland, Givetian; Alberta, Canada, Givetian; Dinant Basin, Belgium, Eifelian; Guangxi, China, Eifelian.

REMARKS. Continuous laminae, characteristic chain-like pillar cross sections and their variability in interlaminar space are identical with *A. fallax* Lecompte. Preservation in some specimens is poor, with parallel zones of skeleton obliterated. Thus only a small sample was available for morphometric study. *Atelodictyon lazutkini* (Yavorsky, 1955) has less well developed vertical elements. *A. obscurum* (Yavorsky, 1955) has more tortuous pillars in interlaminar space. *A. durum* (Khromych, 1974) has pillar and laminar spacings approaching that of the Burdekin material, but the chain structures do not appear as elongate in the figure provided by Khromych (1974: pl. 15, fig 1.). *A. latitextum* Wang in Wang et al. (1986) has a more amalgamate appearance in tangential section. This taxon has thicker laminae than *A. hickense* Webby, Stearn & Zhen 1993 from the Lower Devonian of Victoria.

Schistodictyon Lessovaya,
in Lessovaya & Zakharova 1970

TYPE SPECIES. *S. posterius* from the Upper Silurian Isfra Beds, Turkestan, by original designation.

REMARKS. Stearn (1991) and Bogoyavlenkaya & Khromych (1985) have provided a discussion and synonymy for this genus. Webby, Stearn & Zhen (1993) have recorded a doubtful representative of this genus from Victoria, Australia. Stearn (1991) discussed *Nexililamina* Mallett, from north Queensland as a possible synonym.

Schistodictyon sp.
(Fig. 23)

MATERIAL. JCUF12014 from L 781.

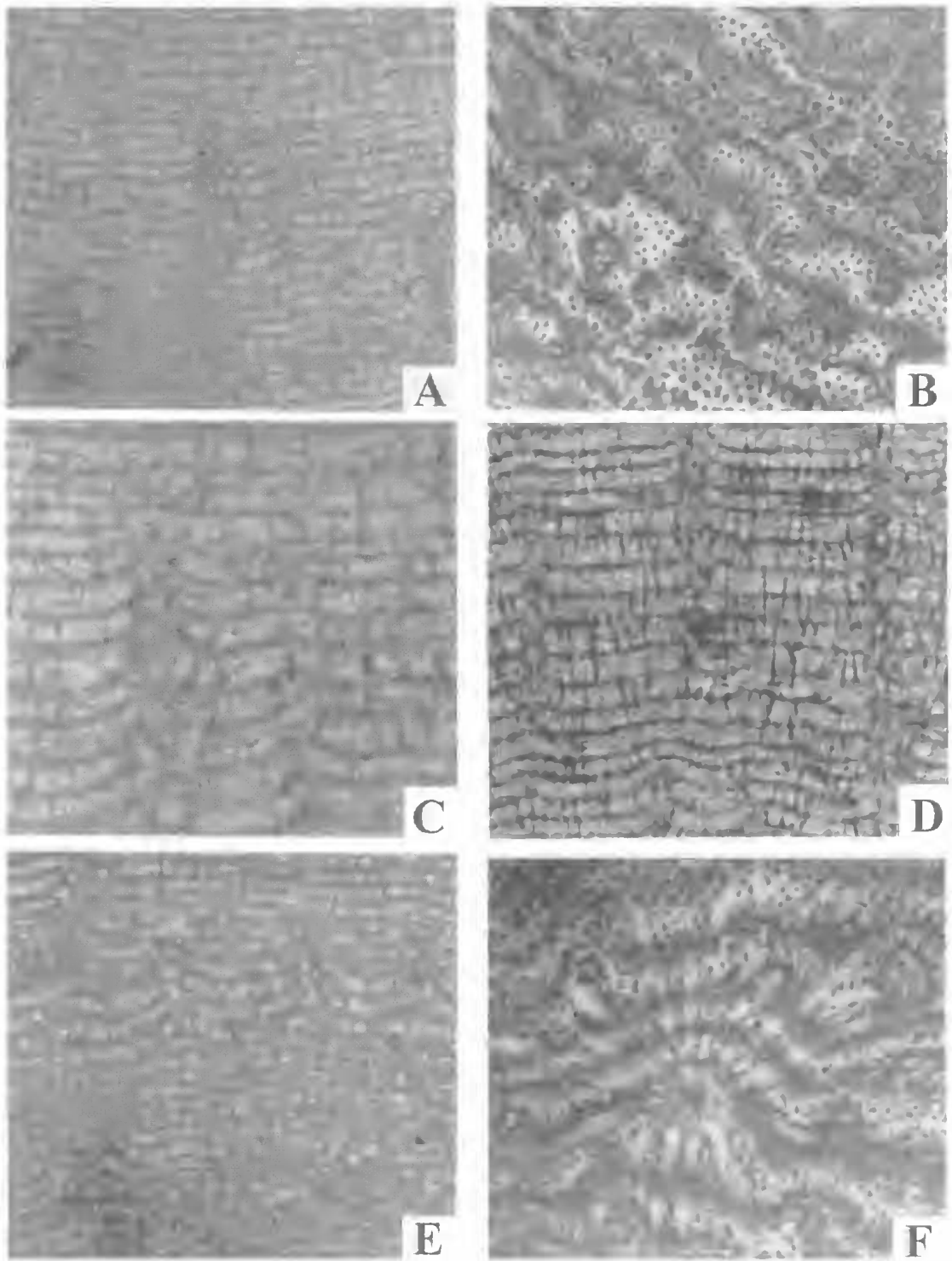DESCRIPTION. Single fragment of a low domical skeleton greater than 4cm wide and 3cm

FIG. 24. *Gerronostroma hendersoni* sp. nov. A-C, holotype JCUF11955 × 10. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, paratype JCUF10817, vertical section × 10; E, F, paratype JCUF11956 × 10; E, vertical section; F, tangential section.

thick. Laminae straight to gently undulose, continuous, each comprised of a dark thin compact line. Laminae 4-7 per 2mm, 0.02-0.05mm thick, highly variably spaced, highlighting thin latilaminae,. Pillars short, not superposed, highly complex within interlaminar space, being multiply branched, commonly oblique, and spreading along the lower surfaces of laminae, irregularly spaced, 7-12 per 2mm, 0.02-0.08mm thick. Skeletal material compact. Galleries irregular, with an overall rectangular to rounded aspect. Weak astrorhizal traces present. There may be dissepiments but these are difficult to distinguish from the complex pillar branches.

REMARKS. Complex branching of pillars is typical of *Schistodictyon*. The specimen lacks the obvious dissepiments of *Pseudoactinodictyon* and the branching is far too simple for *Anostylostroma*. The laminae are not formed by colliculi such as in *Aculatostroma*. *Anostylostroma*? sp. of Mistiaen (1985) is similar in aspect and should be reassigned to *Schistodictyon*. *Nexililamina dipcreekensis* Mallett is of doubtful generic identity (Stearn, 1991), but possible assignment to *Schistodictyon* has been suggested (Stearn, 1980, 1991). It has much simpler interlaminar branching of pillars.

Gerronostroma Yavorsky 1931

Gerronostroma Yavorsky 1931: 1406; Galloway & St. Jean 1957: 151; Galloway 1957: 438; Stearn 1966a : 101; Flügel & Flügel-Kahler 1968: 545; Yang & Dong 1979: 37; Stearn 1980: 889; Bogoyavlenskaya & Khromych 1985: 77; Mistiaen 1985: 127; Stearn 1990: 494; Stock, St. Jean & Otte 1990: 4; Webby & Zhen 1993: 332.

Clathrostroma Yavorsky 1960:

Gerronodictyon Bogoyavlenskaya 1969: 20.

Praeidiostroma Bogoyavlenskaya 1969: 108.

? Gerronostromina Khalfina & Yavorsky 1971: 119.

?Impanodictyon Khalfina & Yavorsky 1971: 119.

TYPE SPECIES. *Gerronostroma elegans* Yavorsky, from the Middle Devonian of the Kuznets Basin, Russian Federation by subsequent designation of Galloway & St Jean (1957).

DISTRIBUTION AND AGE. Old World Realm, Silurian (Ludlow) to Late Devonian (Frasnian).

Gerronostroma hendersoni sp. nov.
(Figs 24, 25A)

ETYMOLOGY. For Professor Robert Arthur Henderson, of James Cook University, Townsville, for his contribution to the palaeontology of north Queensland, and to this study.

MATERIAL. HOLOTYPE: JCUF11955 from JCUL781. PARATYPES: JCUF11944, 11945, 11946, 11949, 11950, 11956 from JCUL778; JCUF11948, 11951, 11952,

11958, 11965, 11967, 11969, 11970 from JCUL779; JCUF 1194, 11953, 11954, 11957, 11959, 11961, 11962, 11964, 11968, 11971, 11972, 11975 from JCUL781; JCUF11960 from JCUL784; JCUF11963, 11966 from JCUL788; JCUF11973, 11974 from JCUL795.

DIAGNOSIS. *Gerronostroma* with laminae spaced 6-10 in 2mm, pillars 6-11 in 2mm; with commonly inflected laminae, with infections giving rise to small persistent tubes and common dissepiments which may be locally continuous.

DESCRIPTION. Skeleton laminar, low or medium domical, up to 140mm high and 200mm wide; some material fragmental. Commonly latilaminate with latilaminae 2-5mm thick. Astrorhizae common, inconspicuous to absent in hand specimen, revealed in tangential section as complex but small (3-9mm wide), with no observed partitions within canals. Vertical sections consist of strongly to weakly undulose laminae, locally inflected. These upturnings sporadically form continuous vertical tubes which traverse many laminae. Laminae continuous, spaced 6 to 10 in 2mm (mean = 8.04, σ= 1.08, N=50),0.02mm to 0.15mm thick (mean = 0.10, σ=0.03, N=50); single-layered and compact or transversely fibrous. Pillars superposed through up to 10 laminae forming a grid, and consist of compact or fibrous skeletal material, spool-shaped, 0.03 to 0.13 mm thick (mean =0.1, σ=0.04, n=50), spaced 6 to 11 in 2mm (mean =8.6, σ=1.5, n=50). Galleries are slightly vertically elongated. Gently arcuate to near straight dissepiments are present in interlaminar spaces of some specimens, where they may be locally continuous producing microlaminae. Others are more arcuate and discontinuous.

In tangential section pillars rounded or coalesced to short vermicular in form. Laminar intersections a continuous sheet, rarely pierced by pores. Laminar inflections, where present are evidenced by complex ring structures 0.3-1.2mm across (mean =0.7, σ=0.3, n=21), or where inflections are up to one interlaminar space in height, simple rings resembling ring pillars (mean =0.32, σ=0.06, n=23) are apparent.

MORPHOMETRICS.

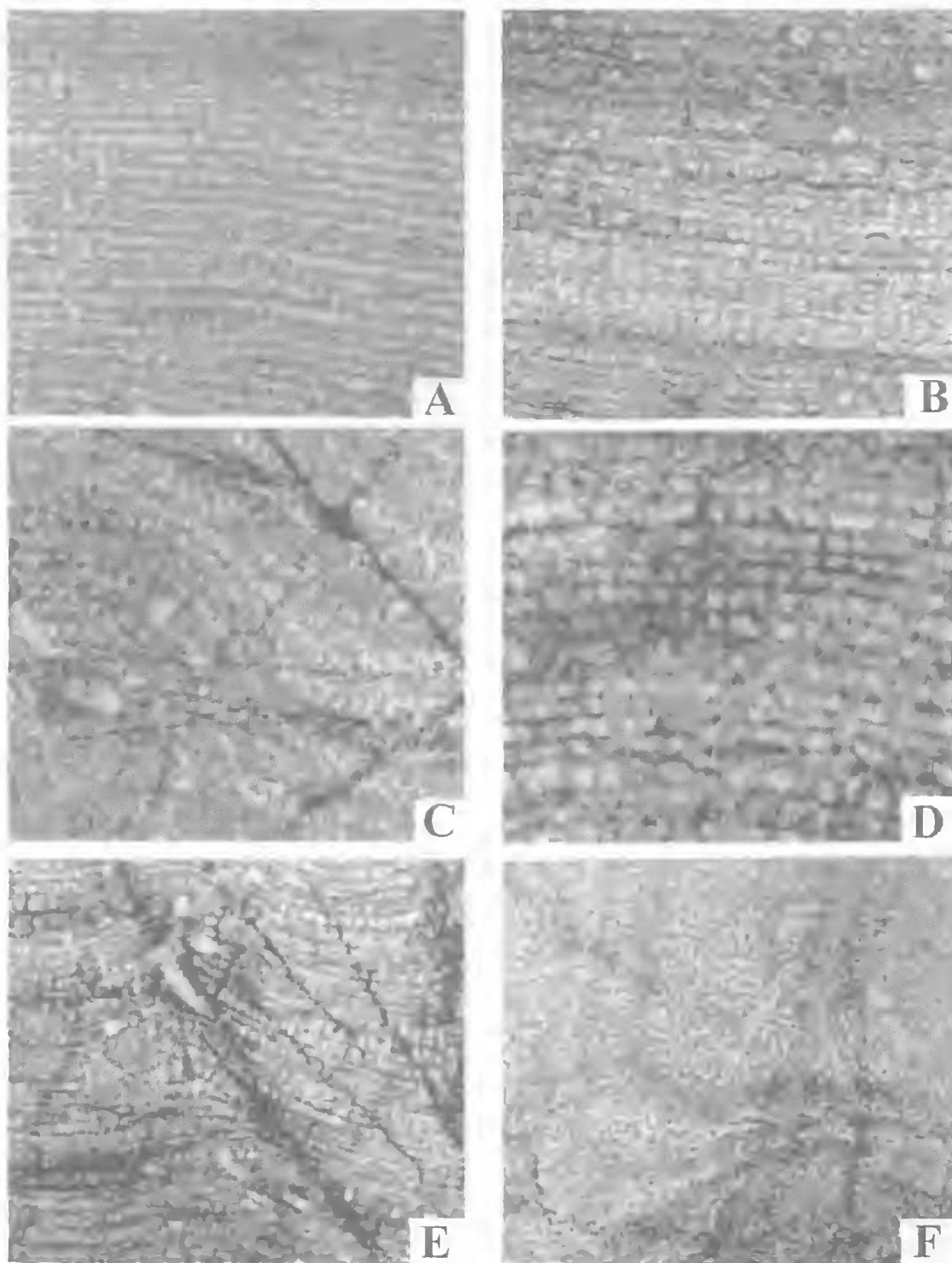| Specimen	L2	L1	P2	P1	n
JCUF11951	8.1(0.9)	0.09(0.03)	7.3(1.5)	0.10(0.03)	10
JCUF11954	8.4(0.7)	0.08(0.02)	8.3(1.2)	0.08(0.03)	10
JCUF11955	7.9(1.2)	0.08(0.04)	9.0(1.2)	0.11(0.03)	10
JCUF11957	7.3(1.1)	0.10(0.03)	9.4(1.2)	0.12(0.05)	10
JCUF11969	8.5(0.9)	0.12(0.05)	9.0(1.2)	0.11(0.04)	10
Average	8.0 (1.0)	0.09 (0.03)	8.6 (1.3)	0.10 (0.04)	-

FIG. 25. A, *Gerronostroma hendersoni* sp. nov. Paratype JCUF11973, vertical section ×10. B-F, *Gerronostroma* sp. B-D, JCUF11978. B, vertical section x 10; C, tangential section × 10; D, vertical section × 20. E, F, JCUF11977. E, vertical section × 10; F, tangential section × 10.

DISTRIBUTION AND AGE. Burdekin Formation, north Queensland, Middle Devonian, Givetian.

REMARKS. The regular grid, persistent laminae and spool-shaped, superposed pillars, clearly identify *Gerronostroma* Yavorsky. Burdekin material differs from other *Gerronostroma* by pillar and laminar spacings, laminar inflections and the slightly elongate galleries. Species closest to this taxon are *Gerronostroma* cf. *G. immemoratum* Bogoyavlenskaya of Stearn (1983) which resembles the Burdekin material in element spacing, but lacks the inflected laminae, and the common dissepiments. *G. immemoratum* Bogoyavlenskaya is also comparable, but also lacks the laminar inflections. The published illustrations (Bogoyavlenskaya 1977b) are too poor for an adequate assessment of relationships.

Presence of 3 orders of tube-like structures within specimens is problematic. Ring pillars are regarded as a generic character of *Stromatoporella* Nicholson, but the regular superposition of the pillars, and the absence of tripartite laminae in the Burdekin material excluded this genus. Persistence of these tubes in vertical section suggests that they may represent a very simple astrorhizal tube, with no radiating canals. If this were so then they may be of little taxonomic value. In addition one may expect a gradation from small tubes to complex canal systems. More complex ring structures are expressions of small mamelons, clearly represented in vertical section, and the largest order structure is naturally the astrorhizae. There is no ontogenetic development from small tubes through complex rings to astrorhizae in this material, and they are not gradational features. Some laminar inflections associated with the small tubes are half to one laminar interspace in height, and are best regarded as expressions of micromamelons on the contemporary surface. Others show no relief from their contemporary surfaces and are problematic.

Gerronostroma sp.
(Fig. 25B-F)

MATERIAL. JCUF11977-82, 12009, 12015-6. All from JCUL788 except JCUF11979 from JCUL779 and JCUF11982 from JCUL781.

DESCRIPTION. Low to medium domical skeleton. Two specimens show intergrowth with rugose corals (JCUF12016 with cf. *Stringophyllum* sp. and JCUF11978 with an unidentified form). Latilaminae are inconspicuous, between 1-2mm thick, with a basal zone of more closely spaced laminae. Adjacent to coral intergrowths in JCUF12016 the grid becomes highly disorganised and skeletal structure becomes a dense complex array of elements. In vertical section, pillars and laminae form a regular grid. Laminae continuous, slightly undulose, or locally undulose suggesting low mamelons, 8-11 per 2mm and 0.02-0.08mm thick. Pillars mostly continuous, through up to 7 laminae, but sporadically they are restricted to interlaminar space, commonly slightly spool-shaped between laminae, spaced 8-11 per 2mm, 0.02-0.08mm thick. Galleries equidimensional to slightly vertically elongate, rectangular with common rounded corners; no dissepiments were seen within them. In tangential section pillars isolated to short vermiform. Laminar intersections appear as sweeping arcuate zones of dense material sporadically pierced by irregular voids. In JCUF12016, where intergrown with rugose corals, the pillars are poorly preserved but show irregular form and spacing; mostly vermiform and a little narrower in cross-section. Astrorhizae small and simple with a central rounded axial canal and up to 4 short, thick simple radiating canals lacking dissepiments. Skeletal material, although not very well preserved appears to be compact.

REMARKS. The species differs from the type by the spacing of pillars and laminae, and in *G. elegans* Yavorksy the pillars are 2-3 times thicker than the laminae. *G. hendersoni* sp. nov. has fewer pillars and laminae per 2mm, problematic tubular structures, and possesses dissepiments. *G. vergens* Webby & Zhen, 1993 from the Emsian Jesse Limestone, New South Wales, has similar pillar-laminar spacing but possesses more prominently V-shaped pillars. Due to the indifferent preservation of this material, the taxon is left in open nomenclature.

Anostylostroma Parks, 1936

TYPE SPECIES. *Anostylostroma hamiltonense* by monotypy, from the Middle Devonian Traverse Group, Michigan, U.S.A.

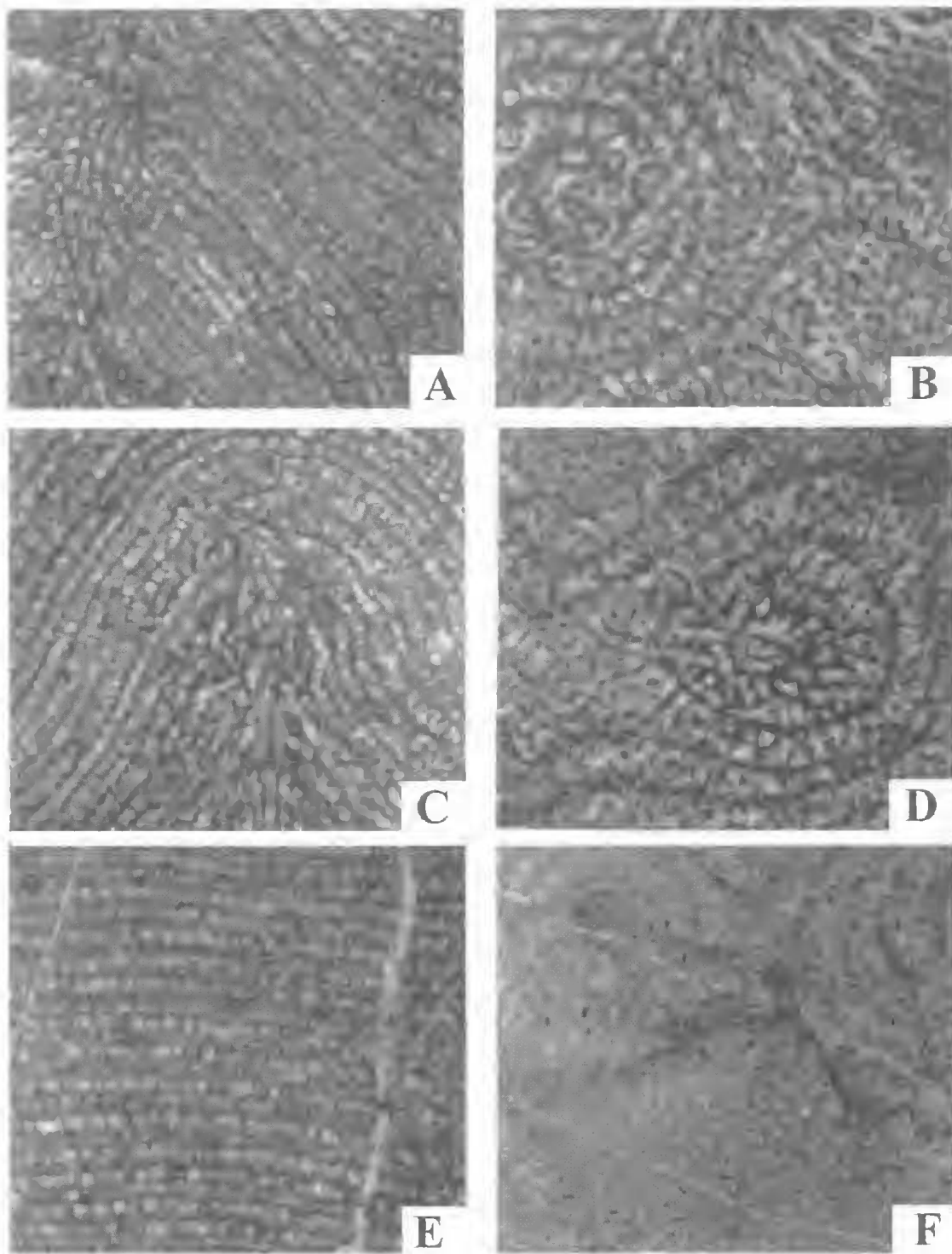REMARKS. A recent review has been presented by Stearn (1991) and further comment is unnecessary.

FIG. 26. A-D, *Anostylostroma ponderosum* (Nicholsun, 1875) JCUF11379 × 10. A, C, vertical section; B, D, tangential section. E, F, *Anostylostroma* sp. JCUF12005 × 10. E, vertical section; F, tangential section.

Anostylostroma ponderosum
(Nicholson, 1875)
(Fig. 26A-D)

Stromatopora ponderosa Nicholson 1875: 246, pl. 24, figs. 4,4a,4b.
Clathrodictyon ponderosum Parks 1936: 42, pl. 5, figs. 5,6.
Anostylostroma ponderosum (Nicholson) 1957: Galloway & St. Jean: 111, pl. 4, figs. 2a, 2b; Fagerstrom 1962: 425, pl. 65, figs. 1-8; Stearn & Mehotra 1970: 6, pl 1, figs. 1,2; Kazmierczak 1971: 81,pl. 14, figs. 2a,2b,3; Cockbain 1984: 24, pl. 8a-8d.

MATERIAL. JCUF11379-82 all from JCUL778.

DESCRIPTION. Material consists of fragments derived from low domical to laminar skeletons, weakly latilaminate. Continuous, strongly undulating, laminae relatively thin, average 13 per 5mm, average thickness 0.07mm. Pillars in some cases superposed and flaring upwards, some branch in interlaminar spaces, approximately 16-17 per 5mm, varying greatly in thickness (average 0.07mm). Dissepiments very common, but not omnipresent. Tissue compact. Mamelon columns very prominent 13-17mm apart showing a variable diameter. In vertical section the skeletal elements within columns merge, intertwine, commonly fuse and inflected upwards. Columns appear as a disorganised collection of vertical vermiform 'tubes.' Intercolumnar skeleton comprises somewhat vermiform pillars which distributed 9-10 per $1mm^2$. Astrorhizal canals present but inconspicuous and are found within mamelon columns.

MORPHOMETRICS.
Pl^2= number of pillars per 1mm square in tangential section

Specimen	P2	L2	Pt	Lt	Pl^2
JCUF11379	6.5	5.2	0.07	0.07	10.6
JCUF11380	7.2	6.8	0.10	0.12	8.0
JCUF11381	6	5.6	0.08	0.07	9.6
JCUF11382	8	5.4	0.08	0.11	9.2

DISTRIBUTION AND AGE. Canning Basin, Western Australia, Frasnian; Burdekin Sub-province, north Queensland, Givetian; Holy Cross Mountains, Poland, Frasnian; Italy, Middle Devonian; Ohio and Michigan, Middle Devonian; Ontario, Canada, Middle Devonian; Northwest Canada, Frasnian.

REMARKS. The flaring and/or branching of the pillars in interlaminar space and the characteristic mamelon columns places the specimens within *Anostylostroma ponderosum*

(Nicholson). Fagerstrom (1982) and Cockbain (1984) have discussed the synonymy of *A. ponderosum* and *A. laxum*. The solution to the problem of types suggested by Cockbain (1984) remains unresolved; no type has, as yet, been chosen from the type locality. Morphometric data indicated some degree of variation within the species with JCUF11380 and JCUF11382 possessing thicker skeletal elements and representing specimens that have experienced more pronounced diagenetic effects. A similar phenomenon was reported for the genus by Fagerstrom (1982).

Anostylostroma sp.
(Figs 26E,F, 27A,B)

MATERIAL. JCUF12005-7, 12010-13, ?JCUF12008 all from JCUL788.

DESCRIPTION. Skeletal shape medium domical up to 7cm thick and 12cm wide; some smaller fragmental material. Astrorhizae inconspicuous in hand specimen. Latilaminae present but not obvious, 0.8-3.0cm thick. Laminae and pillars form a regular grid in vertical section. Laminae thin, 0.02-0.08mm thick, continuous, dark and compact, 6-10 per 2mm. Pillars compact, mostly superposed forming a grid, straight or commonly branched in interlaminar space into a y-shape or flaring along the base of laminae, thicker than laminae (0.05-0.10mm), 8-10 per 2mm. Galleries rectangular to irregular, lacking dissepiments. Astrorhizal axial canals wide, generally straight, with thick compact strongly arcuate dissepiments. In tangential section pillars very rarely isolated, mostly forming short linked chains of short vermiculae. Arcuate laminar intersections are somewhat diffuse. Astrorhizae inconspicuous, consisting of scattered walled radial canals with few dissepiments and wide circular intersections of axial canals.

REMARKS. Predominance of superposed pillars in this taxon suggests reference to *Gerronostroma* but the common Y-shaped pillars indicates affinities to *Anostylostroma* whose type species also has superposed pillars. *G. vergens* Webby & Zhen has similarly y-shaped pillars in a comparable network. Webby & Zhen (1993) suggested their taxon may be *Schistodictyon*, but that genus is characterised by far more complexly branched pillars. *G. vergens* may well represent *Anostylostroma*, despite its regular skeletal network. Poor preservation of all the available material
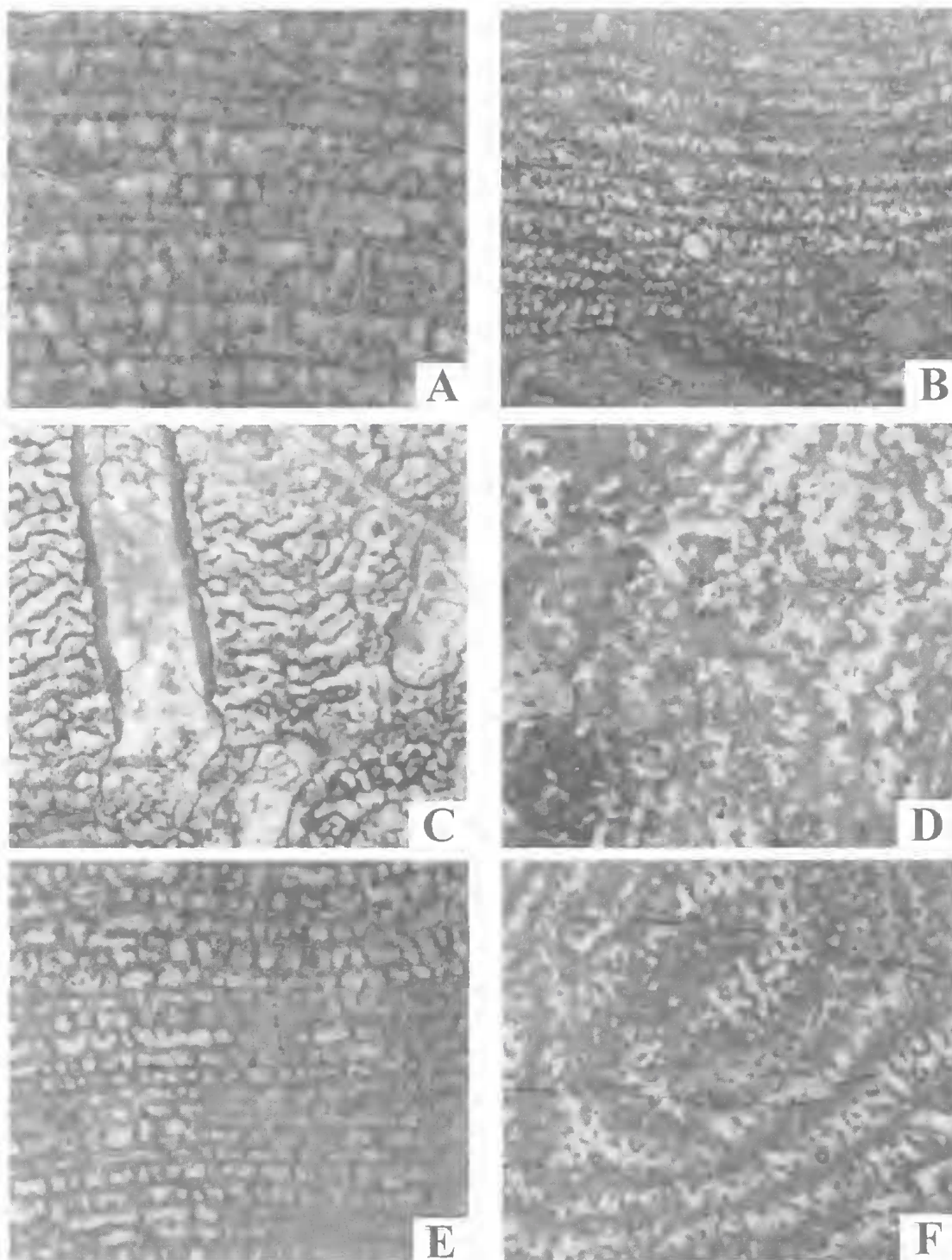
FIG. 27. A, B, *Anostylostroma* sp. A, JCUF12005, vertical section × 20; B, JCUF12006, oblique-vertical section × 10. C, D, Gen. et. sp. indet. cf. *Clathrodictyella* sp. JCUF11378 × 10. C, vertical section; D, tangential section. E, F, *Stictostroma* sp. JCUF11976 × 10. E, vertical section; F, tangential section.

precludes proper definition of this taxon but the unusual style of regular network suggests reference to a new species.

Genus et species indet. cf. **Clathrodictyella** sp.
(Fig. 27C,D)

MATERIAL. JCUF11378 from JCUL778.

DESCRIPTION. Small fragment of a presumably laminar skeleton possessing a symbiotic tabulate coral of syringoporid affinity. Prominent, thick, discontinuous laminae, undulatose and locally chevroned throughout, 12 to 13 per 5mm and are 0.08 to 0.2mm thick; weakly inflected giving off a few, generally thinner, variable pillars confined to one interlaminar space. Pillars spaced 6-7 per 5mm, 0.05-0.15mm thick, cateniform in tangential section. Microstructure mostly compact with a very weak fibrous nature.

REMARKS. This single specimen does not relate well to all other specimens within the Burdekin collections. Professor Colin Stearn (pers. comm.) has viewed copies of the illustrations herein and suggested a relationship to *Clathrodictyella* Bogoyavlenskaya or *Novitella* Bogoyavlenskaya whose species are mostly cylindrical in skeletal shape. The specimen is referred tentatively to *Clathrodictyella* on the basis of the gross skeletal element morphology, but the problem of a non-cylindrical skeleton remains unresolved.

STROMATOPORELLIDA Stearn, 1980
STROMATOPORELLIDAE
Lecompte, 1952

Stictostroma Parks, 1936

TYPE SPECIES. *Stictostroma mammiliferum* Galloway & St. Jean, 1957 (cf. Fagerstrom 1977).

Stictostroma sp.
(Fig. 27E,F)

MATERIAL. JCUF11976.

DESCRIPTION. Skeletal shape very low domical with maximum height 30mm maximum width 170mm, terminal surface gently undulose; with scattered small astrorhizae. In vertical section the skeleton is dominated by relatively continuous, undulating laminae spaced 14-17 per 5mm, sporadically pierced by pores. Laminae 0.15-0.20mm thick, conspicuously tripartite with upper and lower margins of compact material separating a light axial zone. Laminae commonly

have, coalesced with their margins, circular, hollow 'pustules' approximately 0.15mm in diameter projecting slightly into interlaminar space.

Pillars not superposed, confined to, and commonly not completely crossing, interlaminar space; in many places oblique. Where complete they are spool-shaped, commonly flare upwards or rarely divide, thicker than laminae (0.15-0.3mm) and spaced irregularly at 10-18 per 5mm. Pillars consist of compact to flocculent skeletal material. Galleries irregular, elongate with rounded boundaries, commonly crossed by thin dissepiments. In tangential section pillars rounded to short and vermiform; rare ring-pillars present. Sections through laminae highlight regular, rounded foramina and rarely a light median zone. Astrorhizae are complex, wide, with a centre of regular pillars and laminae and long thick radiating arms not obviously traversed by dissepiments.

REMARKS. The rare presence of ring pillars, the tripartite laminae and non-superposed pillars clearly identifies the specimen as *Stictostroma*. Lack of additional material precludes specific assignment despite the well preserved nature of the specimen and it is left in open nomenclature pending more material.

Clathrocoilona Yavorsky, 1931

Clathrocoilona Yavorsky 1931: 1394; Yavorsky 1955: 38; Galloway & St. Jean 1957: 221; Galloway 1957: 451; Galloway 1960: 634; Stearn 1962: 14; Stearn 1966a: 98; Stearn 1966b: 45; Birkhead 1967: 79; Stearn & Mehrotra 1970: 11; Zukalová 1971: 55; Khromych 1974: 36; Khromych 1976: 54; Kosareva 1976: 21; Dong & Huang 1978: 32; Yang & Dong 1979: 70; Stearn 1980: 891; Stock 1982: 670; Stock 1984: 776; Bogoyavlenskaya & Khromych 1985: 71; Mistiaen 1985: 94; Stock, St. Jean & Oite 1990: 3.
In Part *Stromatoporella* Nicholson, Lecompte 1952: 88.
In Part *Stromatopora* Goldfuss, Kazmierczak 1971: 88 .

TYPE SPECIES. *C. abeona* Yavorsky 1931 by monotypy from the Middle Devonian, S.W. Border of the Kuznetsk Basin, Russia.

DISTRIBUTION. Widely distributed, Eifelian to Famennian.

REMARKS. *Clathrocoilona* has been variably assigned to the Stromatoporellidae, Stromatoporidae, Clathrodictyidae and Stictostromatidae. The problematic relationship between it and like genera such as *Stictostroma*, *Stromatoporella*, and *Synthetostroma* stems from conflicting interpretations of the style and importance of microstructure. Macrostructural similarities between these latter 3 genera led Stearn (1980) to

include them all in the Stictostromatidae. *Stromatoporella* Nicholson possesses ring-pillars, and ordinicellular laminae (Stearn, 1966a). *Clathrocoilona* was separated from *Stictostroma* Parks on the basis of an arbitrary point in morphological gradient, *viz.* when the thickness of the laminae reaches the height of the galleries (Stearn, 1966a). *Synthetostroma* Lecompte was synonymised with *Clathrocoilona* by Kosareva (1976). This is in contrast to the views of Galloway (1957) who noted, as differences, the large number of microlaminae and the presence of superposed pillars in *Synthetostroma*. Lecompte's (1951) original diagnosis is clear: *Synthetostroma* has superposed pillars and cellular skeletal fabric, rather than the seldom superposed pillars and compact tissue of *Clathrocoilona*. Stearn (1980) did not support the opinions of Kosareva (1976), maintaining *Synthetostroma* as a separate genus. Stock, St. Jean and Otte (1990) noted Kosareva's (1976) view and commented that St. Jean disagreed with the synonymy. Given Lecompte's (1951) original diagnosis, it is clear that *Clathrocoilona* and *Synthetostroma* are separate genera.

Yavorsky (1931 & 1955) stressed the importance of the rounded galleries and the compact skeletal tissue for *Clathrocoilona* which combined with the characteristic tripartite laminae are essential to the concept of the genus.

Clathrocoilona abeona Yavorsky, 1931
(Fig. 28A,B)

Clathrocoilona abeona Yavorsky 1931: 1395, 1407, pl. 1, figs. 9-11, pl. 2, figs. 1,2,2a; Rukhin 1938p. 88, pl. 22, fig. 2; Galloway 1957 pl. 3,5, fig. 8; Galloway & St. Jean 1957: 222, pl. 21. fig. 3, pl. 23, fig. 1; Flügel & Flügel-Kahler 1968: 16; Fischbuch 1969: 180, pl. 13, figs. 1-5; Yang & Dong 1979: 71, pl. 39, figs. 5-6; Bogoyavlenskaya & Khromych 1985: 4.
? *Clathrocoilona abeona* Yavorsky, Galloway 1960: 634, pl. 77, fig. 2.

MATERIAL. JCUF 12059, 12063, 12748 and ? 12753 from JCUL778; JCUF 12060-12062, JCUF 12751, 12752 from JCUL781; JCUF 12749 from JCUL788; JCUF 12750 from Golden Valley, S of Fanning River Station.

DESCRIPTION. Skeletal shape laminar to low domical, with a large range in size up to 80cm wide and 8cm thick. Growth surface variably undulose, some specimens showing widely spaced (1-4cm), low mamelons. Specimens moderately, although not conspicuously, latilaminate with latilaminae thicknesses of 0.8-2.5cm. In vertical section skeletal elements form an irregular grid. Laminae continuous, gently to moderately undulose, sporadically

upturned into mamelon columns within which they are difficult to separate from pillars, 3-6 per 2mm, thick (0.18-0.28mm), with a thin, central, light axis. Laminae divide sporadically along their length giving rise to new laminae. The central line similarly divides with the dividing laminae. Pillars are short, thick and spool-shaped, and may be superposed through 2-3 laminae, but in general confined to one interlaminar space. They are irregularly spaced across the laminae (3-6 per 2mm), thinner than laminae, but of variable thickness (0.05-0.25mm). Pillars and laminae are comprised of compact to flocculent tissue, with some suggestions of relict transverse fibrosity. Galleries irregular, rectangular, ovoid or rounded, and generally horizontally elongate; as thick as laminae. Dissepiments are common. Upturnings in laminae give rise to broad mamelon columns within which skeletal material is disordered. Two or more irregular vertical tubes form the vertical expression of the astrorhizae; which may be crossed by dissepiments. In tangential section laminar intersections dominate and consist of solid skeletal material with rare small pores; less commonly a trace of the central light line of the laminae is seen. Pillars are rounded, ovoid to very short, vermiform in cross section and are commonly joined by dissepiments. They commonly coalesce to form larger irregular pillar masses. At margins of laminae they coalesce with the solid skeleton. In tangential section astrorhizae are expressed as wide, diffuse radial sets of, in some places, long, walled thick canals, with or without dissepiments, eminating from a complex central mamelon column. There is no single centre, but a number of rounded central cavities.

DISTRIBUTION AND AGE. SW Kuznets Basin, Russia, Middle Den; Logansport Limestone, Indiana, Middle Devonian; Swan Hills Formation, Canada, Late Givetian; Mackenzie Valley, NWT, Canada, Frasnian.

MORPHOMETRICS.

Specimen	L2	Lt	P2	Pt
JCUF12051	4.0 (0.5)	0.21 (0.04)	5.1 (0.7)	0.15 (0.06)
JCUF12061	4.9 (0.7)	0.20 (0.06)	5.7 (1.3)	0.13 (0.07)
JCUF12062	4.0 (0.6)	0.23 (0.04)	4.9 (0.7)	0.18 (0.09)
JCUF12748	4.1 (0.5)	0.19 (0.05)	5.1 (1.1)	0.13 (0.05)
Average	4.3 (0.7)	0.21 (0.05)	5.2 (1.0)	0.14 (0.07)

REMARKS. This material is indistinguishable from that described by Yavorsky (1931), which
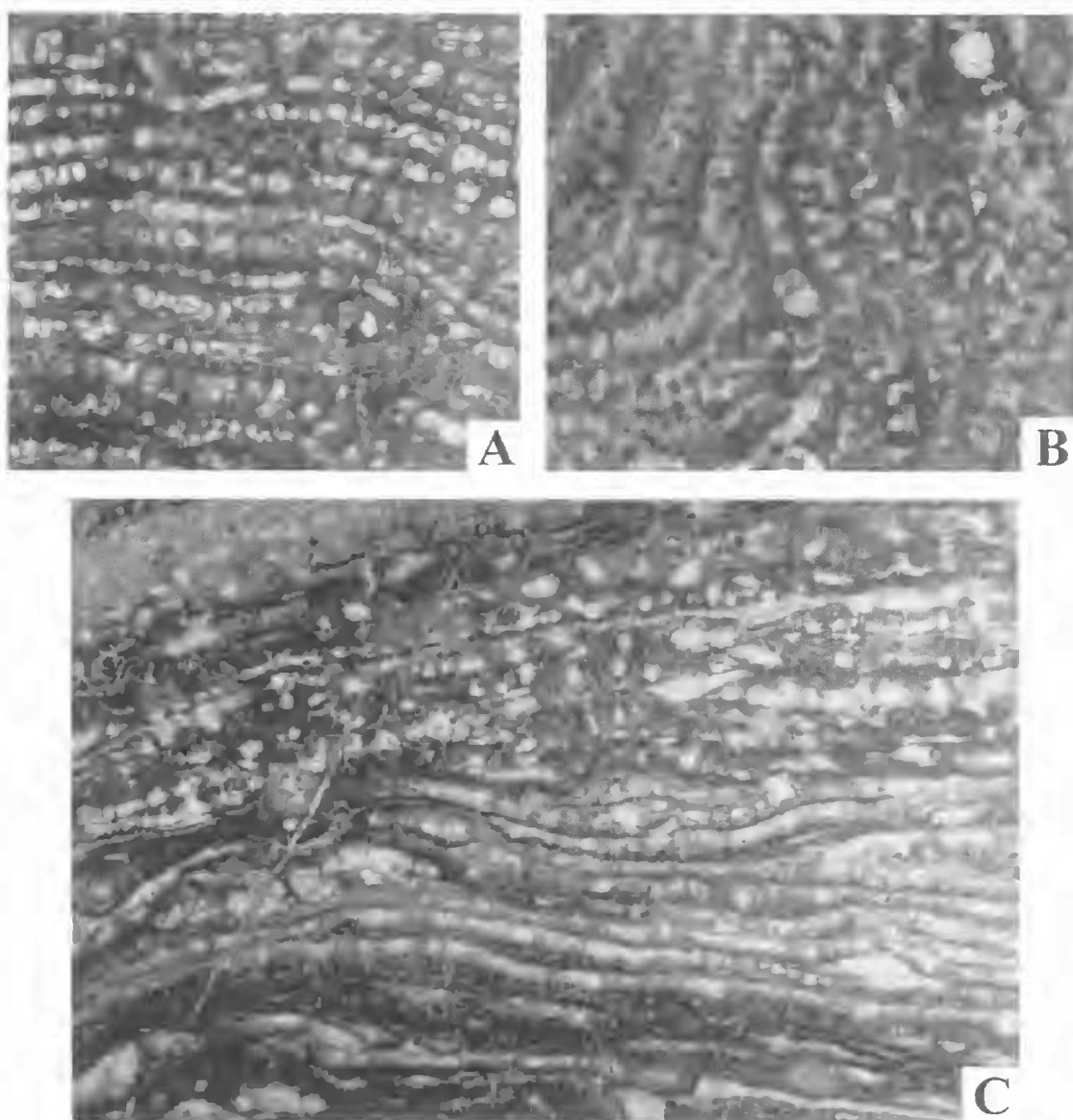
FIG. 28. *Clathrocoilona abeona* Yavorsky 1931 JCUF12750 × 10. A, vertical section; B, tangential section; C, *Clarthrocoilona spissa* (Lecompte, 1951) JCUF11426 × 10, vertical section.

has comparable pillar and laminar spacings, irregular galleries, element thicknesses and astrorhizal development. *C. spissa* (Lecompte) has more occluded galleries and is more solid in tangential section. *C. saginata* (Lecompte) has a finer, more regular grid network, and in tangential section skeletal elements are better differentiated. Fischbuch (1969) placed *Stromatoporella irregularis* Lecompte in synonymy with this taxon. It is viewed here as

closer to *C. spissa*, given the more irregular nature of the galleries.

Clathrocoilona spissa (Lecompte, 1951)
(Figs 28C, 29)

Stromatoporella spissa Lecompte 1951: 187, pl. 37, figs 3-4. Kazmierczak 1971: 92, pl. 21, figs. 2a-b.
Clathrocoilona cf. *spissa* (Lecompte), Stearn 1961: 945, pl. 107, figs. 7-8:
Clathrocoilona spissa (Lecompte) Zukalová 1971: 56, pl. 15, figs. 1-2: Flügel 1974:, 165, pl. 24, figs. 2,4, pl. 26,
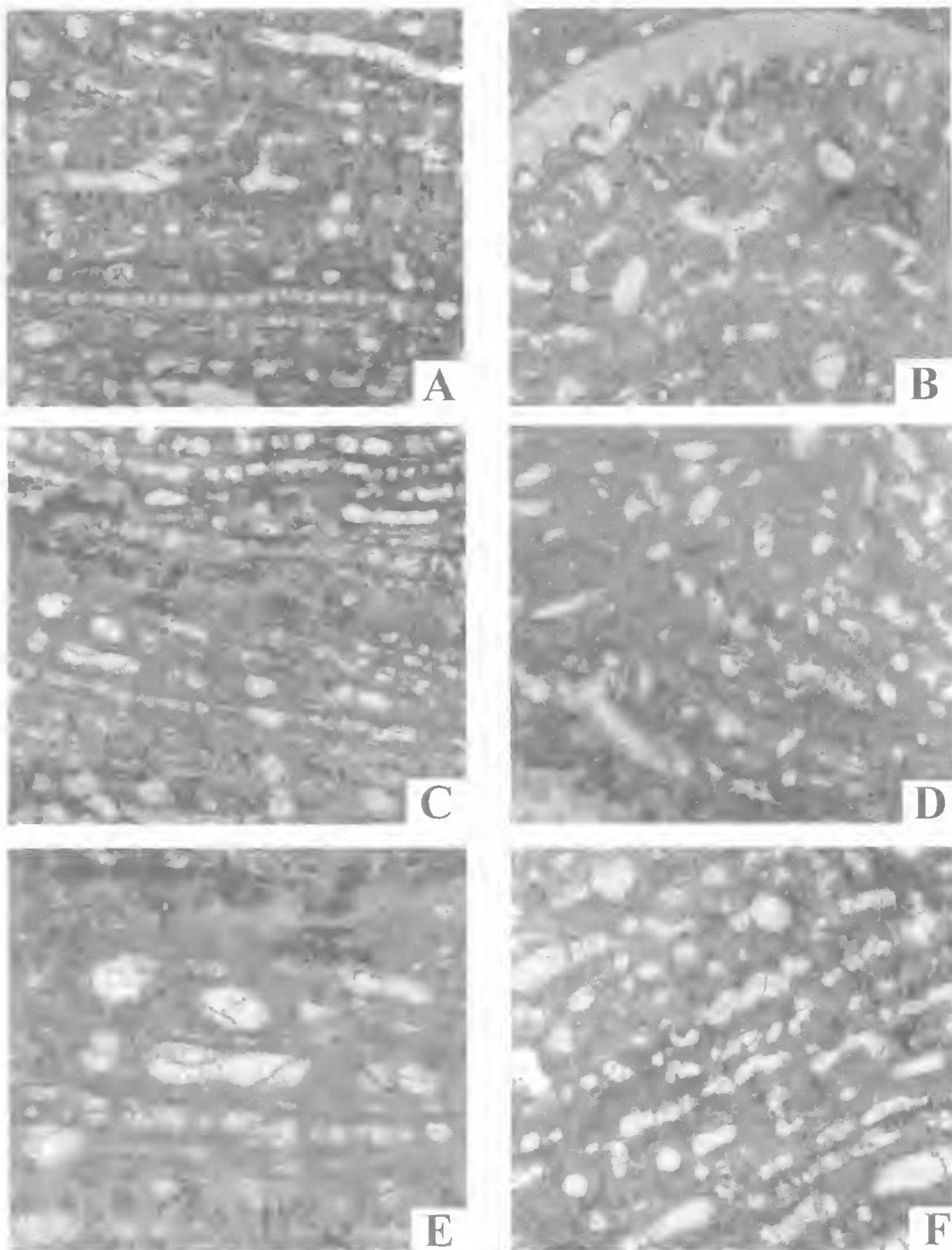
FIG. 29. *Clathrocoilona spisa* (Lecompte, 1951). A, B, JCUF11421. A, vertical section × 10; B, tangential section × 10. C, D, JCUF11432. C, vertical section × 10; D, tangential section × 10. E, F, JCUF11428. E, vertical section × 10; F, tangential section × 10.

fig. 4, pl. 27, fig. 5; Mistiaen 1980: 196, pl.7, figs. 3-9; Cockbain 1984: 25, pl. 11a-d; Mistiaen 1985:. 96, pl. 6, figs. 6-8: Mistiaen 1988: 174, no figs.
? *Clathrocoilona, ? Stromatoporella spissa* Lecompte, Flügel & Flügel-Kahler 1968: 534, p. 399.

MATERIAL. JCUF11413-18, 11420-32, all from JCUL788.

DESCRIPTION. Skeleton thin, laminar, generally encrusting, in general strongly latilaminate. Base of each latilamina has a somewhat ordered array of skeletal elements 1 to 2 laminae thick in which laminae are continuous, commonly with a light median layer, and compact pillars that are spool-shaped and rarely superposed. This gives way to a much thickened amalgamate network in which tissue occupies approximately 70% of the skeleton. Pillars and laminae are difficult to differentiate. Galleries small, rounded or elongated, and 0.1-0.3mm high. They often extend upwards to form 'coenotubes' several laminae high (up to 1mm) or traverse laminae obliquely forming part of astrorhizae. The galleries are commonly crossed by dissepiments. In tangential section skeletal elements dominate, astrorhizal systems are obvious and galleries appear vermicular, up to 0.5mm wide. Microstructure is compact to flocculent.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Middle Devonian (Givetian);Boulonnais, France, Middle to Late Devonian (Givetian to Frasnian); Dinant Basin, Belgium, Middle to Late Devonian (Givetian to Frasnian); Holy Cross Mountains, Poland, Middle to Late Devonian (Givetian to Frasnian); Afghanistan, Late Devonian (Frasnian); Moravian Karst, Czechoslovakia, Late Devonian (Frasnian); Canning Basin, Western Australia, Late Devonian (Frasnian).

REMARKS. The thickened skeletal elements, the laminae with a median light line, and the diminished galleries are consistent with *Clathrocoilona Yavorsky*, and in particular with *C. spissa* (Lecompte, 1951). *C. spissa* (Lecompte, 1951) differs from other species of *Clathrocoilona* by the density of skeletal architecture, especially in tangential section, the obliteration of galleries, the characteristic latilamination, the vertically elongate galleries and the oblique astrorhizal tubes. Mistiaen (1988) doubted the assignment of Canning Basin material referred by Cockbain (1984) to *C. spissa* (Lecompte, 1951). Mistiaen (1985, 1988) regarded figures 11c and d of Cockbain (1984) as

more like *C. obliterata* (Lecompte, 1951). Cockbain's (1984) figures do not relate well to Lecompte's (1951) illustrations of *Stromatoporella obliterata*, and his original identification of the Canning material is supported. Inspection of some of Cockbain's original material has confirmed this view.

HERMATOSTROMATIDAE
Nestor, 1964

Hermatostroma Nicholson, 1886b

Hermatostroma Nicholson 1886b: 105; Lecompte 1952: 247; Yavorsky 1955: 140; Lecompte 1956: F131; Galloway & St Jean 1957: 217; Galloway 1957: 451; Galloway 1960: 635; Stearn 1966a: 106; Stearn 1966b: 59; Birkhead 1967: 78; St. Jean 1967: 424; Flügel & Flügel-Kahler 1968: 547; Fischbuch 1969: 171; Kazmierczak 1971: 122;:Zukalová 1971: 80; Khromych 1974: 41; Flügel 1974: 170; Khromych 1976: 65; Yang & Dong 1979: 67; Mistiaen 1980: 202; Stearn 1980: 842; Stock 1982: 664; Dong 1983: 293; Bogoyavlenskaya & Khromych 1985: 78; Dong 1988: 31; Stock, St. Jean & Otte 1990: 5.

TYPE SPECIES. *Hermatostroma schlueteri* Nicholson, 1886b, by monotypy, from the Middle Devonian of the Paffrath District, Germany.

DISTRIBUTION AND AGE. Widely distributed through the Old world and Eastern Americas Realm late Early to Late Devonian.

REMARKS. The genus *Hermatostroma* Nicholson 1886b, with type species *H. schlueteri*, from the Middle Devonian of Paffrath, Germany, has found considerable usage with a large number of assigned species. A major problem with this genus is the interpretation of its microstructure, and in particular, the conflict between forms with cellular microstructure (melanospheric to some authors) and to those with compact skeletal material and marginal vesicles, cellules and peripheral membranes.

Webby, Stearn & Zhen (1993) have placed Ripper's (1937d) 2 species of *Hermatostroma* within *Pseudotrupetostroma. Stromatoporella loomberensis* Dun in Benson (1918) is undoubtedly a *Hermatostroma*, as noted by Flügel & Flügel-Kahler (1968). Cockbain (1984) described *H. ambiguum* Cockbain, *H. perseptatum* Lecompte, *H. roemeri* (Nicholson) and *H. schlueteri* Nicholson from the Canning Basin.

There appears to be a consensus on the higher level systematics of this genus, with most authors reflecting the view that the hermatostromatids are a family level grouping (Bogoyavlenskaya, 1969; Khalfina and Yavorsky, 1971; Stearn, 1980).
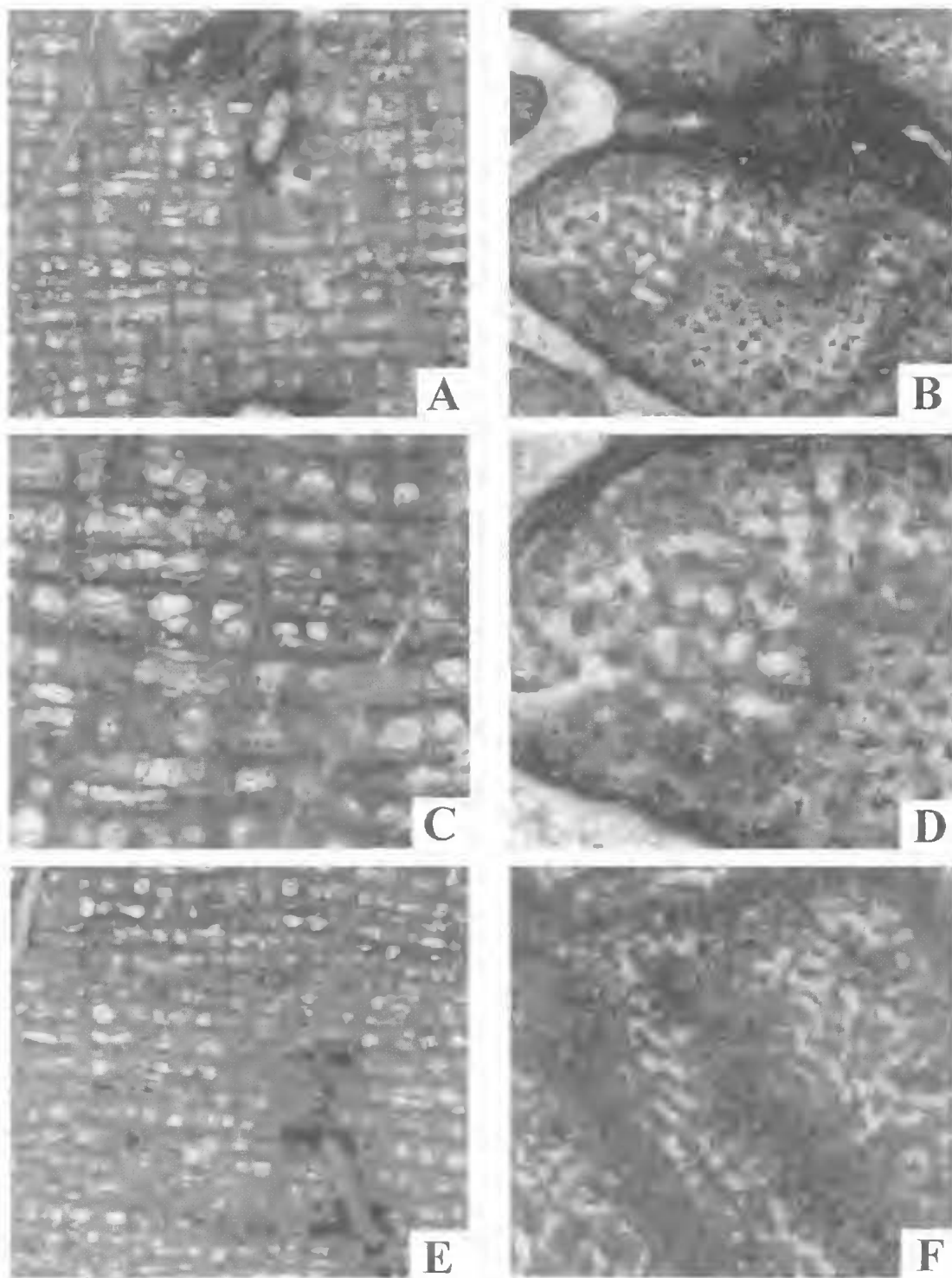
FIG. 30. *Hermatostroma episcopale* Nicholson, 1892. A, D, JCUF11856. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, JCUF11855. E, tan vertical section × 10; F, tangential section × 10.

Hermatostroma episcopale Nicholson, 1892
(Figs 30, 31)

Hermatostroma episcopale Nicholson 1892: 219, pl. 28, figs. 4-11; Lecompte 1952: 216, pl. 48, fig. 4, pl. 49, figs. 1-2; Galloway 1960: 635, pl. 77, figs 4a,b; Yang & Dong 1963: 162, pl.10, figs 3-6; Zukalová 1971: 82, pl. 11, figs. 5,6, pl. 27, figs. 1,2; Kazmierczak 1971: 124, pl. 8, fig. 6, pl. 34, figs. 2a,b; Yang & Dong 1979: 68, pl. 32, figs. 7,8; Bogoyavlenskaya & Khromych 1985: 20.
Not *Hermatostroma episcopale* Nicholson, Ripper 1937d:. 29, pl. 5, figs. 7-8.

MATERIAL. JCUF11853-8, 11863-5, 11873 from JCUL787, JCUF11859-62, 11894, 11900 from JCUL794, JCUF11867, 11870, 11890, 11893, 11896, 11899 from JCUL778, JCUF11869, 11872, 11897-8 from JCUL779, JCUF11866, 11868, 11891-2 from JCUL781, JCUF11871 from JCUL793, JCUF11874 from JCUL788, JCUF11895 from JCUL796.

DESCRIPTION. Skeletal shape thick laminar to low domical, maximum width 21cm and maximum height 9cm, not obviously latilaminate. Skeletal elements form a highly regular grid in vertical section. Laminae continuous, gently undulose, 11-18 per 5mm, and 0.05-0.20mm thick with a persistent, thin, dark, compact central line and light margins or well developed peripheral membranes. Pillars continuous, superposed and spool-shaped in interlaminar spaces. Peripheral membranes extend onto pillar margins, but pillars lack the dark central line of the laminae. Pillars spaced 10-15 per 5mm, 0.15-0.28mm thick. Galleries rectangular with rounded margins produced by peripheral membranes or lighter peripheral material on laminae. Abundant arcuate, compact dissepiments. In tangential section, laminar cross sections appear as sweeping bands of diffusely melanospheric skeletal material commonly with a diffuse central dark zone. Where isolated, pillars are rounded to short vermiform in outline, and often joined by dissepiments. Membranes around pillar elements rarely preserved in tangential section where skeletal material often has a melanospheric appearance. No obvious astrorhizae in the specimens.

MORPHOMETRICS.

Specimen	P5	Pt	L5	Lt
JCUF11855	12.8 (1.0)	0.20 (0.03)	15.3 (1.1)	0.16 (0.05)
JCUF11856	13.4 (1.2)	0.15 (0.04)	13.7 (1.1)	0.15 (0.03)
JCUF11862	13.3 (1.8)	0.16 (0.02)	13.0 (1.7)	0.15 (0.04)
JCUF11865	14.1 (1.6)	0.19 (0.04)	12.5 (0.9)	0.18 (0.05)
Average	13.4 (1.6)	0.17 (0.04)	13.6 (1.6)	0.16 (0.04)

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Devon, U.K., Middle Devonian; Dinant Basin, Belgium, Frasnian; Holy Cross Mountains, Poland, Givetian-Frasnian; Moravian Karst, Czechoslovakia, Givetian-Frasnian; Gueizhou, China, Givetian; Guangxi, China, Givetian; Xizang, China, Frasnian.

REMARKS. The regular grid and peripheral membranes or light margins allies this material to *Hermatostroma*. The pillar-laminar spacing, the abundant dissepiments and the unusual microstructure are inseparable from *H. episcopale*. This species differs from *H. maculatum* by the pillar-laminar spacing, and the abundant dissepiments, and microstructural characteristics. *H. episcopale* has a much more open network than *H. ambiguum* .

Hermatostroma maculatum
Yang & Dong, 1979
(Figs 32, 33)

Hermatostroma maculatum Yang & Dong 1979: 67, pl. 38, figs 3-4.

MATERIAL. JCUF 11904-11907, 11909, 11910, 11914, ?11921 from JCUL779; JCUF 11908, 11911 - 11913, 11916, 11917, ?, 11923-11925, 11927 and ?, 11918, ?11919, ?11920, ?11926 from JCUL781; JCUF 11915 from JCUL795.

DESCRIPTION. Skeletal shape variable, most commonly low domical or thick laminar. Laminae continuous, gently undulating, 14-22 per 5 mm (mean = 19.1, σ= 1.9, n= 40); 0.09-0.23 mm thick (mean = 0.16, σ= 0.03, n= 40), with prominent dark median line, peripheral membranes and light margins or marginal vesicles. Pillars spool-shaped, superposed, 15-23 per 5 mm (mean = 17.4, σ= 2.2, n= 40), and are 0.08-0.28mm thick (mean = 0.14, σ= 0.04, n=40); commonly with lighter margins or peripheral membranes. Galleries rounded due to preponderance of peripheral membranes, generally longer than high, uncommonly crossed by dissepiments. Tissue compact. Astrorhizae 5-7 mm across, with numerous dissepiments in longitudinal section.

MORPHOMETRICS.

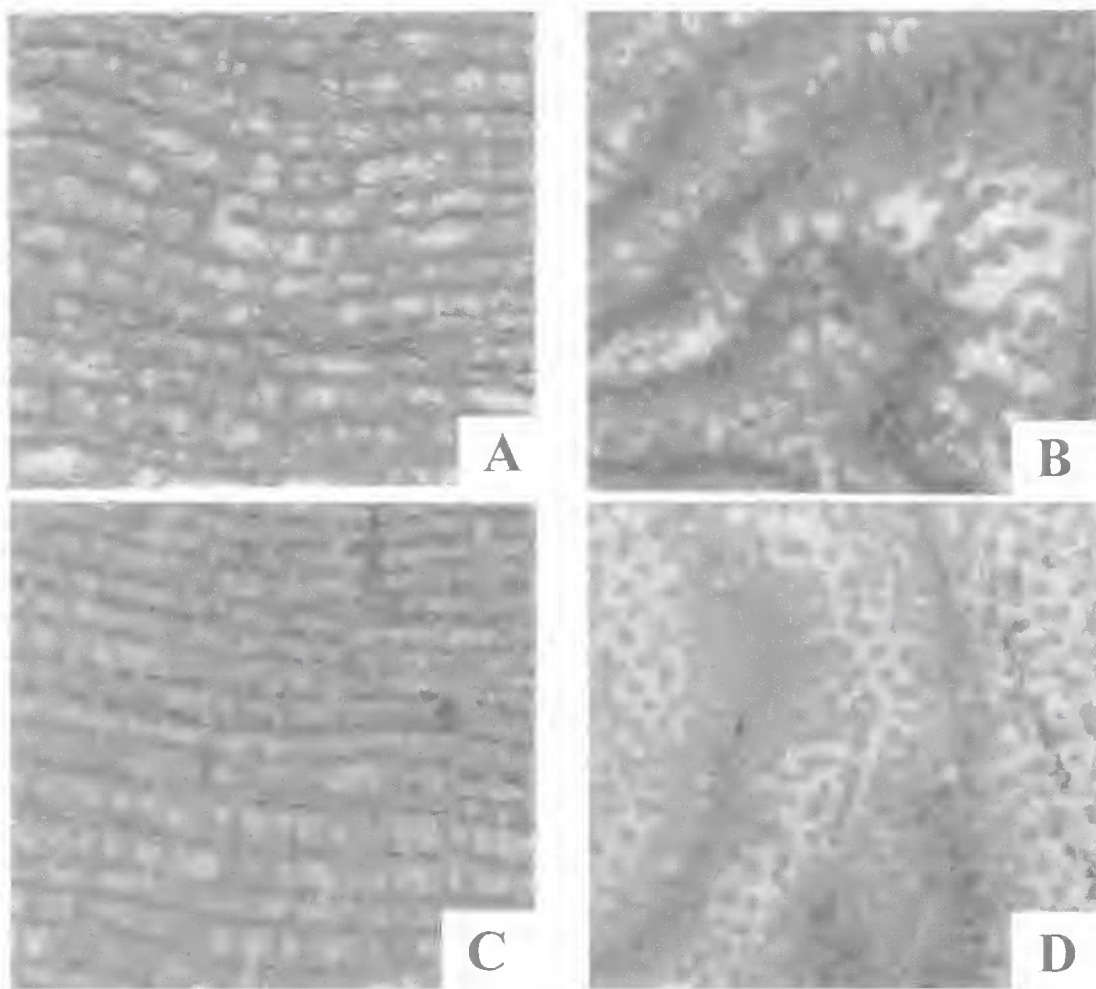| Specimen	P5	Pt	L5	Lt
JCUF11830	16.0 (1.2)	0.15 (0.05)	19.8 (1.6)	0.16 (0.03)
JCUF11836	19.1 (1.4)	0.13 (0.01)	17.6 (0.9)	0.14 (0.05)
JCUF11838	18.3 (2.3)	0.14 (0.03)	20.1 (1.6)	0.16 (0.03)
JCUF11839	16.1 (1.2)	0.15 (0.03)	18.7 (2.2)	0.17 (0.02)
Average	17.4 (0.2)	0.14 (0.04)	19.1 (1.9)	0.16 (0.02)

FIG. 31. *Hermatostroma espiscopale* Nicholson, 1892. A, B, JCUF11865 × 10. A, vertical section; B, tangential section. C, D, JCUF11862 × 10. C, vertical section; D, tangential section.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Guangxi, China, Givetian.

REMARKS. Presence of distinct peripheral membranes, marginal vesicles and light margins in skeletal elements within the same thin section highlights the variable character of the genus. The dominance of membranes places it within *Hermatostroma*. The spacing of skeletal elements and the relative scarcity of dissepiments (compared to other *Hermatostroma* from the Burdekin Formation) identifies the material as conspecific with *H. maculatum* Yang & Dong 1979. It is separated from other Burdekin *Hermatostroma* by the spacing of pillars and laminae and the paucity of dissepiments.

Trupetostroma Parks, 1936

Trupetostroma Parks 1936: 52: Kuhn 1939 p. A44: LeMaitre 1949: 519:Lecompte 1952: 219: Lecompte 1956: F132: Galloway & St. Jean 1957: 158: Galloway 1957: 439: Khalfina 1960: 342: Khalfina 1960: 59: Galloway 1960: 624: Galloway & Ehlers 1960: 58: Stearn 1962: 3: Stearn 1963: 657: Yavorsky 1963: 66: Stearn 1966a: 102: Stearn 1966b: 49: Birkhead 1967: 60: Flügel & Flügel-Kahler 1968: 580: Zukalová 1971: 74: Kazmierczak 1971: 111: Stearn 1975: 1652: Khromych 1976: 66: Yang & Dong 1979: 40: Stock 1982: 665: Bogoyavlenskaya & Khromych 1985: 92: Stock, St. Jean and Otte 1990: 8.

TYPE SPECIES. *Trupetostroma warreni* Parks, 1936, p. 52, pl. 10, figs. 1-2, by original designation from the Middle Devonian of Slave Lake.
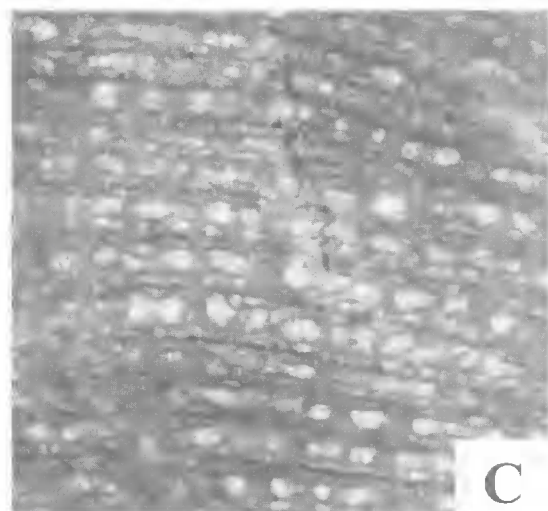
DISTRIBUTION AND AGE. Widely distributed, Early to Late Devonian (Frasnian).
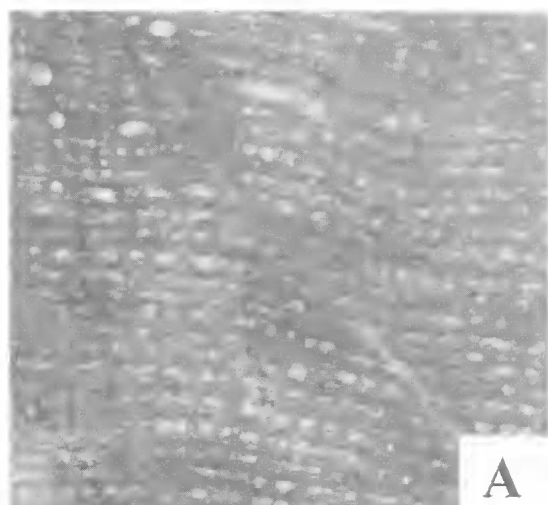
A
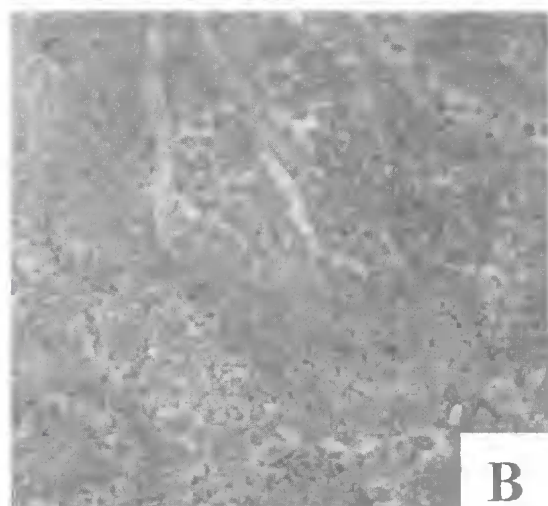
B

C

REMARKS. *Trupetostroma* has been well documented by many authors and requires no additional detailed comment. A number of authors have described dendroid members of the genus. These include *Idiostroma mclearni* Stearn (1962) regarded as *Trupetostroma* by Fischbuch (1970b) and Cockbain (1984), and *T. ernoides* and *T. keratodendroides*, described by Fischbuch (1970) from the Swan Hills Formation, Canada.

Trupetostroma zheni sp. nov.
(Fig. 34A-E)

ETYMOLOGY. The trivial name is for Zhen Yong Yi who so thoroughly described the rugose corals of the Fanning River Group.

MATERIAL. HOLOTYPE: JCUF11765 from JCUL784. PARATYPES: JCUF11767-11769 from JCUL784; JCUF11766, 11770, 11771 from JCUL778.

DIAGNOSIS. Robustly stachyodiform *Trupetostroma* with regular open macrostructure, concentric thick laminae and spool-shaped, superposed pillars.

DESCRIPTION. Skeleton robustly stachyodiform with branch diameters up to 14mm. Pillars spool-shaped, most commonly superposed, 0.12-0.13mm thick, 6-6.4 per 2mm. Laminae concentrically disposed, continuous and relatively thick (0.11-0.13mm), 7-8.5 per 2mm, sporadically pierced by vacuoles. Tissue compact. Within the axial zone of the skeleton the pillars are short and vermiform. A questionable axial canal is present within each of JCUF11768 (0.1mm), JCUF11769 (0.3mm), and JCUF11765 (0.3mm) but is absent in other specimens.

MORPHOMETRICS. (n=5 for each)

Specimen	P2	Pt	L2	Lt
JCUF11768	6.2 (1.2)	0.13 (0.03)	8.0 (0.9)	0.13 (0.03)
JCUF11769	6.0 (0.9)	0.12 (0.02)	8.4 (0.5)	0.13 (0.03)
JCUF11765	6.4 (0.5)	0.14 (0.03)	7.2 (1.0)	0.12 (0.03)

DISTRIBUTION AND AGE. Burdekin Formation, north Queensland, Middle Devonian, Givetian.

REMARKS. Reference to *Trupetostroma* is indicated by the presence of a light axial zone within the laminae and conspicuously spool-shaped pillars, and is reinforced by the

FIG. 32. *Hermatostroma maculatum* Yang & Dong, 1979. JCUF11838, A, vertical section × 10; B, tangential section x 10; C, vertical section × 20.
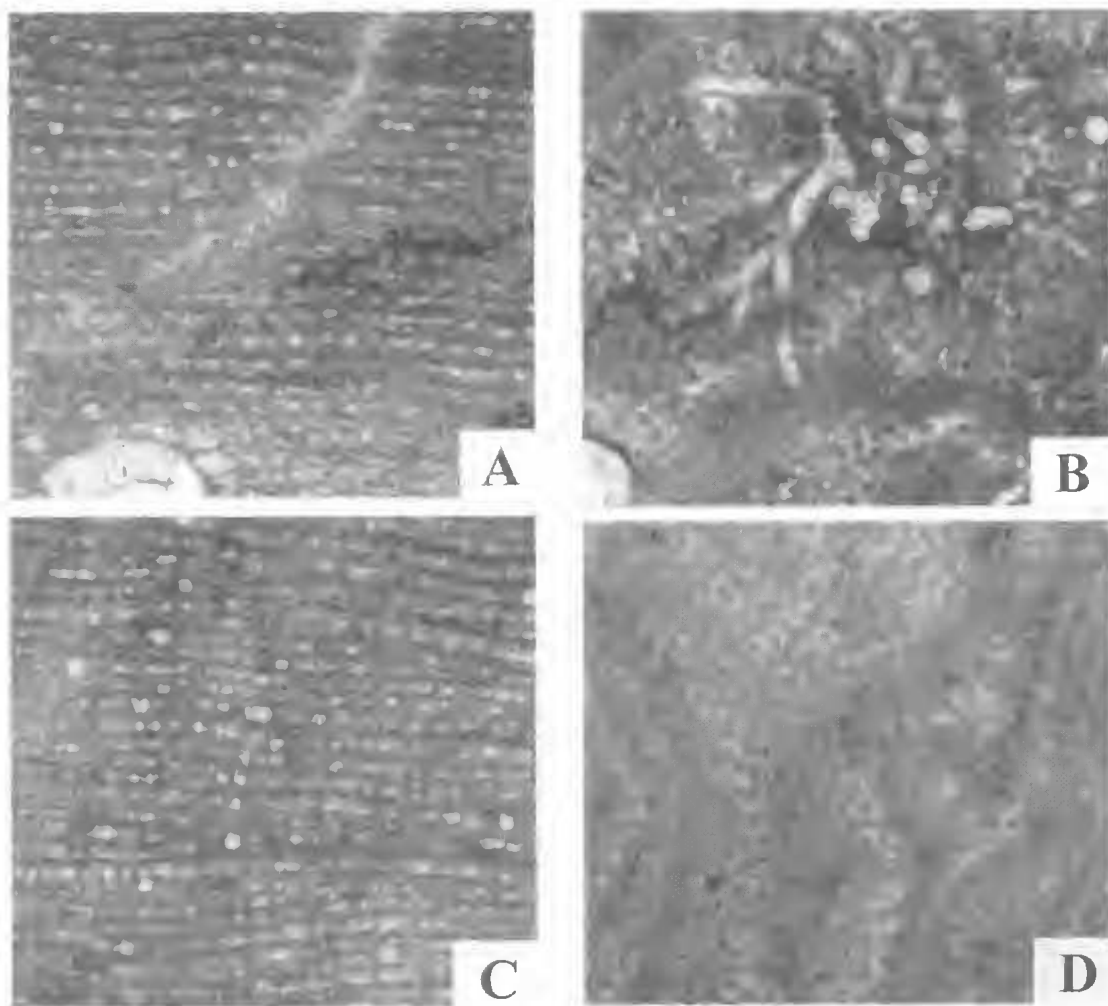
FIG. 33. *Hermatostroma maculatum* Yang & Dong, 1979. A, B, JCUF11832. A, vertical section × 10; B, tangential section × 10. C, D, JCUF11830. C, vertical section × 10; D, tangential section × 10.

presence of poorly developed vacuoles in JCUF11768. This species differs from most other species of *Trupetostroma* in its characteristically robustly dendroid skeleton. *T. mclearni* (Stearn, 1962) possesses a better developed axial canal, and the skeletal architecture is not as well differentiated. *T. ernodes* Fischbuch has a wide, disordered axial zone, missing in this taxon. *T. keratodendroides* Fischbuch has a prominent axial canal and thicker pillars.

The specimens are broadly comparable with *Hermatostroma roemeri* (Nicholson) but this species has a much more prominent axial canal and clearly developed marginal vesicles. They superficially resemble *Idiostroma* aff. *uralicum* Yavorsky but this species has much shorter

pillars which are not as well superposed and is much smaller. The former characteristic was that used by Zukalová (1971) to place *Idiostroma* aff. *uralicum* within *Dendrostroma*. *Dendrostroma oculatum* (Nicholson) grossly resembles *T. zheni* but lacks superposed pillars.

AMPHIPORIDA Ruhkin, 1938
AMPHIPORIDAE Rukhin, 1938

Amphipora Schulz, 1883

Amphipora Schulz 1883, p. 89. (not seen); Nicholson 1886b: 109; Etheridge 1917: 239; Chi 1940: 312; Lecompte 1952: 321; Yavorsky 1955: 149; Gogolczyk 1956: 211; Lecompte 1956: F142; Galloway 1957: 442; Galloway & Ehlers 1960: 97; Stearn 1966: 109; Birkhead 1967: 83; Fischbuch 1970a: 68; Zukalová

1971: 10; Stearn 1980: 831; Stock 1982: 660; Stock, St. Jean & Otte 1990: 2. Stearn, 1997:833.
Paramphipora Yavorsky 1955: 154.
Haraamphipora Rukhin 1938: 93.
Not *Amphipora* Schulz, Ripper 1937a: 37.

TYPE SPECIES. *Caunopora ramosa* Phillips, 1841 from the Middle Devonian of Chudleigh, Devon, England by monotypy.

DISTRIBUTION. Widely distributed, Emsian to Famennian.

REMARKS. Stearn (1997) reviewed the concept of the genus and type species and provides a full generic synonymy.

Amphipora ramosa (Phillips, 1841)
(Fig. 35A-H)

Caunopora ramosa Phillips 1841: 19, pl. 8, fig. 22.
Amphipora ramosa (Phillips), Schulz 1883: 246, pl. 22, fig. 5-6 pl. 23, fig. 1; Nicholson 1886b: 109, 223, pl. 9, fig. 1-4. pl. 29, fig. 3-5; Felix 1905: 73, fig. 1-3; Riabinin 1931: 508, pl. 1, figs. 11-13, fig. 1; Chi 1940: 312, pl. 5, fig. 1-4.Yu 1947; 125 pl. 1, fig. 2a,b: Lecompte 1952: 325, pl. 67, fig. 3. pl. 68., fig. 1-3; Fontaine 1955: 57, pl. 1, fig. 1-4; Yavorsky 1955: 152, pl. 82, fig. 1-4, pl. 84, fig. 2-3; Gogoloczyk 1956: 224 pl. 2, fig. 1-4, text fig. 2-4; Galloway & St Jean 1957: 233, pl. 23, fig. 2-6; Yavorsky 1957: 63, pl.41, fig. 1-9; Galloway & Ehlers 1960: 98, pl. 11, fig. 1a,b; Yavorsky 1961: 68, pl. 38, fig. 15, pl. 37, figs 1-10; Stearn 1961: 946, pl. 107, figs 9,10; Stearn 1963: 663, pl. 87, fig. 2; Stearn 1966: 63, pl. 24, fig. 2; Flügel & Flügel-Kahler 1968: 342;Fischbuch 1970: 69, pl. 15, figs. 1-5; Stearn & Mehrotra 1970: 19, pl. 4, fig. 2; Khromych 1971: 133, pl. 36, fig. 7; Zukalová 1971: 117, pl. 37, fig. 1, pl. 38, fig. 1-4, pl. 40, fig. 2; Stearn 1975: 1665; Yang & Dong 1979: 79, pl. 43, figs. 7,8; Bogoyavlenskaya & Khromych 1985: 48; Khromych & Hung 1988: 31, pl 14, figs. 5-6. Stearn 1997: 845, figs 1-11.
Amphipora ramosa (Phillips). *minor* Riabinin, Khromych 1976: 74, pl. 14,fig. 3; Wang & Huang, 1985: 411,pl. 2, figs 3,4.
Amphipora ramosa (?)(Phillips), Fagerstrom 1982p. 35, pl. 6, fig. 5,6,9; Dong & Wang 1982: 26, pl. 16, figs. 6-9.
Not *Amphipora ramosa* (Phillips), Ripper 1937a: 38, pl. 1, pl. 1-3.

MATERIAL. JCUF11467, 11469-75, all from JCUL788.

DISTRIBUTION AND AGE. Worldwide, ?Early Devonian, Middle Devonian (particluarly Givetian) to Frasnian.

DESCRIPTION. Dendroid (amphiporiform) skeletons 5-10cm long, 1.7-4.3mm in diameter (mean = 3.1 mm, σ = 0.5 , n = 105) canaliculate or non-canaliculate, axial canal 0.2-0.7mm in diameter (mean = 0.4 mm, σ = 0.1, n = 65). Prominent marginal vesicles sporadically crossed by thin dissepiments. Axial canal generally less than one-quarter of skeletal diameter, commonly crossed by thin dissepiments. Microstructure is fibrous from a dark central line within the centre of the skeleton, and fibrous without the dark central line in peripheral skeletal elements.

MORPHOMETRICS. Skeletal diameters and, where possible, axial canal diameters were measured from thin sections. Minimum diameters were taken for slightly oblique sections. All thin sections show multiple skeletons. A summary of data from the material is presented below, the relationships of canal diameter to branch diameter are shown in Figs 36 and 37.

| Specimen	D mean	Dσ	n	A mean	Aσ	n	% canal
JCUF11467	2.9	0.4	16	0.35	0.06	8	50
JCUF11469	3.3	0.4	7	0.47	0.13	5	71
JCUF11470	2.7	0.2	7	0.38	0.07	6	86
JCUF11471	3.2	0.5	6	0.46	0.14	5	81
JCUF11472	2.9	0.5	27	0.36	0.10	11	41
JCUF11473	3.4	0.4	15	0.42	0.08	12	80
JCUF11474	3.4	0.4	14	0.38	0.08	9	64

REMARKS. The material is indistiguishable from *A. pervesiculata* Lecompte in skeletal organisation and size. *S. rudis* (Lecompte) is comparable but is distinguished by its greater size and radiating skeletal elements. *Paramphipora mangkamensis* Dong, *P. zhougedongensis* Dong and *Amphipora tenuissina* Dong & Wang are of comparable size and cannot be effectively discriminated from *A. pervesiculata*. *P. mangkamensis* of Dong (1981) seems to lack the large marginal vesicles of *A. pervesiculata*, but this distinction requires confirmation. *P. zhougedongensis* Dong has small marginal vesicles and may be conspecific with *A. pervesiculata*. *Amphipora tenuissina* Dong & Wang resembles, and may be synonymous with *A. pervesiculata*.

Although *A. fidelis* Yavorsky of Dong & Wang (1984) shows some smaller marginal vesicles its size and large axial canal strongly suggests that it is conspecific with *A. pervesiculata* Lecompte.

Euryamphipora Klovan, 1966

Euryamphipora Klovan 1966: 14; Flügel & Flügel-Kahler 1968: 544; Fischbuch 1970a: 72; Stearn 1980: 891; Mistiaen 1985: 206; Dong 1988: 32; Stock, St. Jean & Otte 1990: 4.

TYPE SPECIES. *Euryamphipora platyformis* Klovan, 1966 p. 15, pl. 3, figs 4a,b, pl. 4, figs. 1-7, by original designation, from the Frasnian Cooking Lake equivalent of the Leduc Formation, Alberta.
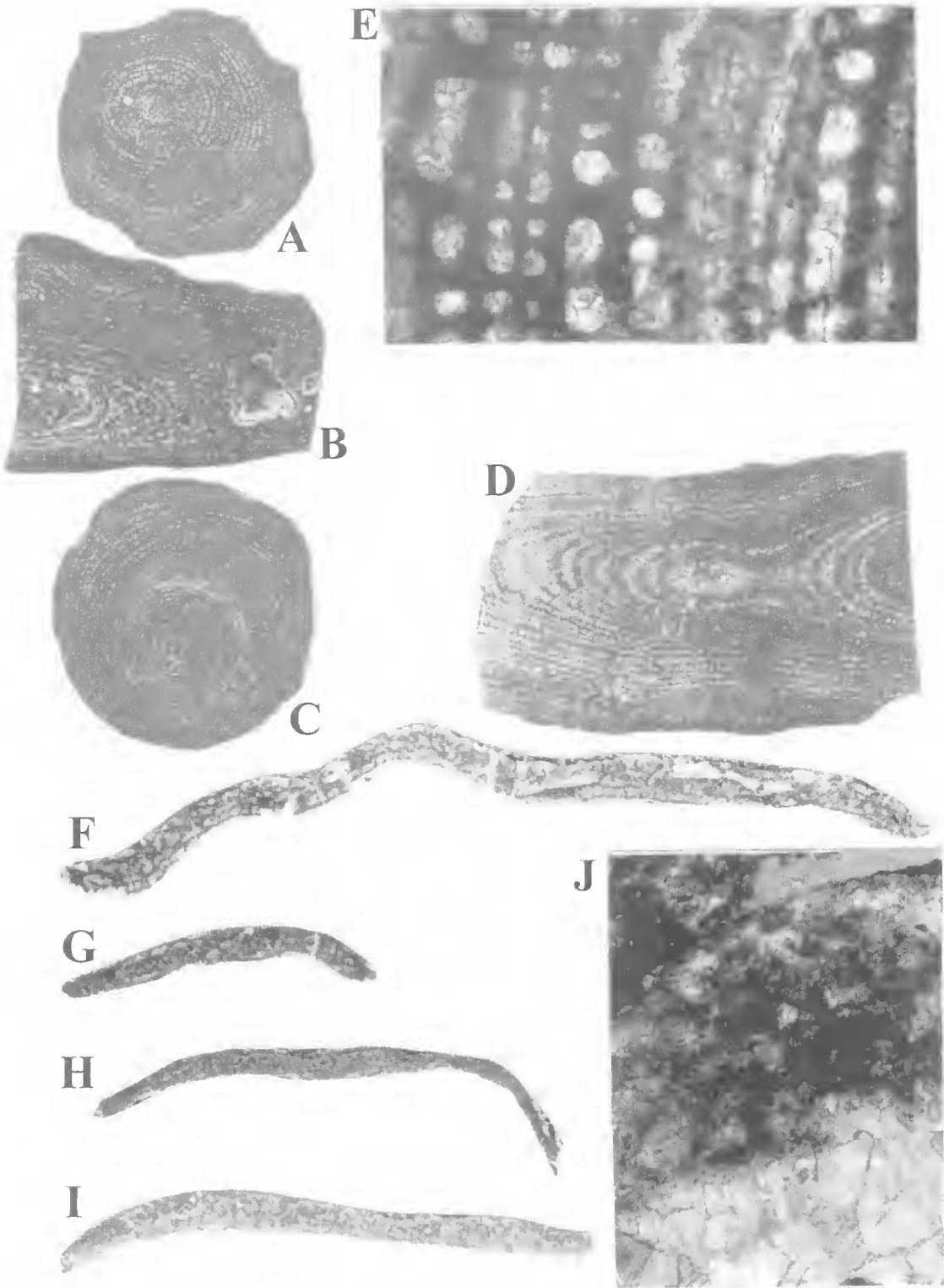
DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia Givetian; Canada, Givetian-Frasnian; Afghanistan, Givetian-Frasnian; Ferques-Boulonnais, France, Frasnian.

REMARKS. *Euryamphipora*, based on *E. platyformis* Klovan, is a little studied and poorly understood genus. *E. mollis* Fischbuch, 1970a, the only other included species, shows a much more delicate structure, more dissepiments and larger marginal vesicles. Cockbain (1984) synonymised *Euryamphipora* with *Amphipora*, regarding it as a laterally compressed *Amphipora*. However the illustrations of Fischbuch (1970a) and Mistiaen (1988) show an obvious platey form. Specimens from the Burdekin Formation are undulose in nature, and quite distinct from associated *Amphipora*. Hence Cockbain's view is rejected.

Euryamphipora merlini sp. nov.
(Fig. 34F-J)

ETYMOLOGY. For Robert Merlin Carter, Professor of Geology, James Cook University of North Queensland.

MATERIAL. Holotype; JCUF11449 from JCUL778, paratypes; JCUF11436, 11438-48 from JCUL778, 780 and JCUF11843-45 from JCUL787.

DIAGNOSIS. Euryamphipora with relatively thick skeletal elements and only moderately inflated upper and lower vesicles.

DESCRIPTION. Skeletal shape thin, laminar, and undulose in encrusting style, 0.7-1.3mm thick, containing only 2 to 5 laminae. Uppermost and lowermost skeletal layer has inflated galleries (vesicles) that are slightly larger than those at the centre of the skeleton. Vesicles 0.1-0.3 mm high. Pillars (0.08-0.12mm) slightly thinner than laminae (0.10-0.14mm) Microstructure transversely fibrous. No dissepiments sighted.

MORPHOMETRICS.

Specimen	Thickness (mm).
JCUF11429	1.3
JCUF11439	0.7, 0.7
JCUF11443	0.7, 0.8, 0.9
JCUF11444	1.2, 0.9, 0.7
JCUF11447	1.3
Average	0.92mm (n=10 σ=0.24)

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Givetian.

REMARKS. The Burdekin specimens differ from *E. platyformis* Klovan, 1966 and *E. mollis* Fischbuch, 1970a in the size of the vesicles, and somewhat thicker skeletal elements. Both *E. platyformis* and *E. mollis* have dissepiments whereas none were found within the Burdekin specimens. No obvious median line within the pillars or laminae has been recognised in *E. merlini,* but the transversely fibrous microstructure is easily recognisable in the holotype and a number of the less altered paratypes. Diagenetic chalcedony has replaced a few of the specimens, and varying degrees of recrystallisation are represented in the suite.

STROMATOPORIDA Stearn, 1980

Stromatopora Goldfuss, 1826

Stromatopora Goldfuss 1826: 21 (not sighted); Winchell 1867: 99; Nicholson 1874: 4; Nicholson 1875: 245; Nicholson & Murie 1878: 217; Bargatzky 1881a: 281; Lecompte 1952: 263; Lecompte 1956: F133; Fritz & Waines 1956: 98; Galloway & Ehlers 1960: 50; Galloway 1960: 627; Flügel & Flügel-Kahler 1968: 568; Khalfina & Yavorsky 1973: 150 (transl.); Stock 1979: 336; Mistiaen 1980: 208; Goldfuss, Stearn: 892; Bogoyavlenskaya & Khromych 1985: 90; Mistiaen 1985: 134; Stearn 1990: 506; Stock, St. Jean, & Otte 1990: 8; Stearn 1993: 210; Webby & Zhen 1993: 344.
? *Stromatopora* Goldfuss, Birkhead 1967: 68.
Not *Stromatopora* Goldfuss, Nicholson 1886b: 23; Galloway & St Jean 1957: 164; Galloway 1957: 447; Stearn 1966a: 110; Stock 1984:778.

TYPE SPECIES. *Stromatopora concentrica* Goldfuss by monotypy, from the Middle Devonian of Gerolstein, Germany.

DISTRIBUTION AND AGE. Widely distibuted, Middle Silurian (Wenlock) to Late Devonian (Famennian) (Stearn 1993).

REMARKS. The genus has been recently reviewed by Stearn (1993) and lengthy discussion is unwarranted. Stearn (1993), following Lecompte (1952) and Mistiaen (1985) stressed the original concept of a cassiculate dominant structure in deference to Nicholson (1886b) who emphasised vertical elements in his concept of the genus. The genus has been distilled by Stearn's (1993) reassessment and now carries

FIG. 34. A-E. *Trupetostroma zheni* sp. nov. A, holotype, JCUF11768, transverse section, × 3; B., holotype, longitudinal section, × 3; C, paratype, JCUF11765 transverse section, × 3; D paratype, JCUF11765, transverse section, × 3; E, holotype, transverse section, × 12. F-J, *Euryamphipora merlini* sp. nov., all longitudinal sections. F, holotype, JCUF11449, × 5: G, JCUF11436, × 5; H, paratype, F11445(a), × 5; I, paratype, JCUF11445(b); J, holotype, JCUF11449, × 30.
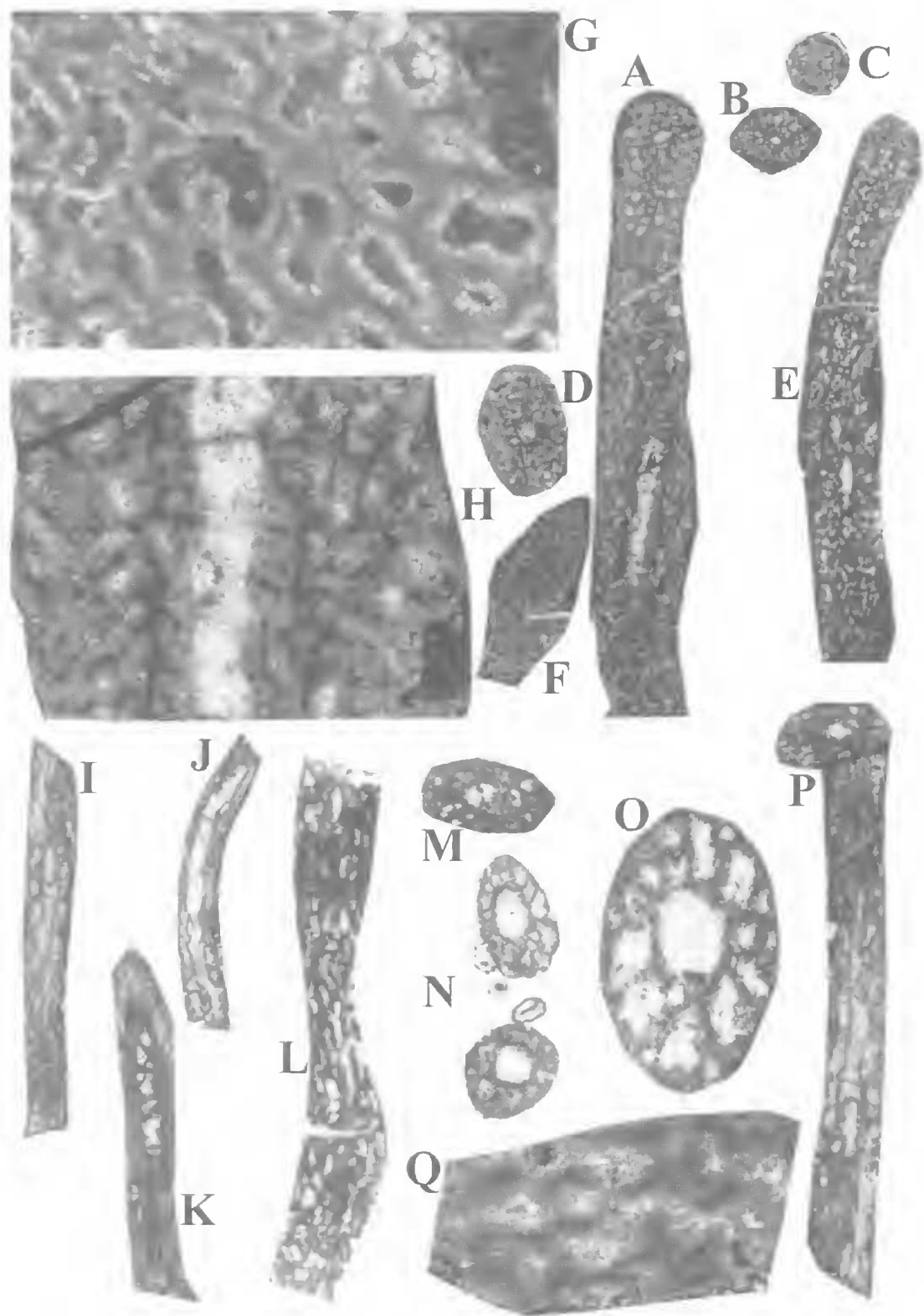
only 26 species, plus 8 doubtful species as opposed to the more than 200 assigned by various authors (cf. Flügel & Flügel-Kahler, 1968; Bogoyavlenskaya & Khromych, 1985). The synonymy list is not exhaustive. Stearn (1993) has provided an extensive synonymy.

Stromatopora huepschii (Bargatzky, 1881a)
(Fig. 40)

Caunopora hüpschii Bargatzky 1881a: 62.
Stromatopora hüpschii (Bargatzky), Nicholson1886b: 26, 92, text fig. 6A,B, pl. 10, figs. 8,9; Nicholson 1891: 176, text fig. 20A, B.pl. 10, figs. 8,9, pl. 22, figs. 3-7; Lecompte 1952: 268, pl. 52, figs. 1-3; Yavorsky 1955: 106, pl. 56, figs. 3-4; Galloway & St. Jean 1957: 168; Galloway 1957: 448, pl. 35, fig. 2; Yavorsky 1961,: 43, pl. 26, figs.4,5; Flügel & Flügel-Kahler 1968: 570; Fischbuch 1969,: 174, pl. 6, figs. 1-5; Yang & Dong 1979: 52, pl. 22, figs. 7,8; Mistiaen 1980: 209, pl. 13, figs. 3-6; Dong & Wang 1982: 52, 19, pl. 10, figs. 5-6; Bogoyavlenskaya & Khromych 1985: 26; Mistiaen 1985: 139, pl. 12, figs. 1-6; Liu & Dong 1991: 318, pl. 2, figs. 4a,b; Dong & Song 1992: 30, pl. 3, figs. 1a,b.
? *Stromatopora alaica* Riabinin 1931: 506, pl. 1, figs. 7,8.
? *Stromatopora sp* cf. *S. huepschii* (Bargatzky), St Jean 1967: 422, pl 1, figs 1-4.
Not *Stromatopora* aff. *S. hüpschii* (Bargatzky), Ripper 1937b: 86, pl. 8, figs. 7,8; Ripper 1937d: 28, pl. 5, figs. 5,6.

MATERIAL. JCUF11772, 11775, 11779, 11780, 11784-6, 11791, 11797-8, 11800-1, 11805, 11928, and 11933 from JCUL788; JCUF11790, 11901, 11929-30 from JCUL787; JCUF11799, 11802-3, and 11902 from JCUL778; JCUF11931 from JCUL794.

DESCRIPTION. Skeletal shape low to medium domical, up to approximately 7cm high and 12cm wide; obscurely latilaminate with latilaminae 0.2-2.5cm thick. Growth surfaces gently to strongly undulose, no obvious mamelons present. In vertical section the structure is a coarse amalgamate network with coenosteles slightly more dominant. Coenosteles short to moderately long, spanning up to 5 coenostromes but mostly less, dominantly erect but a few are oblique, spaced 13-16 per 5mm; very thick, 0.20-0.32mm. Coenostromes of variable length, generally oblique, sporadically persistent along bases of latilaminae, locally replaced by dissepiments. Coenostromes irregularly spaced, making measurement of spacing impossible, a little thinner

(0.15-0.22mm) than coenosteles. Galleries irregular with rounded margins, either vertically lengthened, horizontally elongate or an irregular combination of both, are most commonly crossed by relatively flat dissepiments. Both vertical and horizontal elements coarsely cellular where well preserved, but dissepiments appear compact. In tangential section coenosteles form a labyrinthine network in which galleries range from small and rounded in cross-section to long, irregular and vermiform. No obvious traces of astrorhizae, but sporadically the gallery traces complexly radiate from a central zone, suggesting a diffuse system. Syringoporid symbionts are common in this taxon.

DISTRIBUTION. Germany, Middle Devonian; Spain, Middle Devonian; Italy, Middle Devonian; England, Middle Devonian; France, Givetian; Belgium, Givetian to Frasnian; Kuznetz Basin, Russia, Givetian; Yunnan, China, Givetian; Guangxi, China, Givetian; Xinshau, China, Givetian; Afghanistan, Emsian to Givetian; Alberta, Canada, Givetian; California, United States, undiff. Devonian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. Well preserved specimens are indistiguishable from *S. huepschii* (Bargatzky) as figured by a number of authors including Nicholson (1886b), Lecompte (1952), and Galloway (1957). Lecompte (1952, pl. 52, fig 2,2a,b) figured the type specimen, and although there is dominance of vertical elements in some of the sections and moderate occlusion of the galleries in tangential section, there is sufficient development of a cassiculate network to warrant inclusion in *Stromatopora*. The moderate development of coenostromes precludes assignment to *Salairella*. Material assigned to this species by Ripper (1937b,d) has been reassigned to *Syringostromella zintchenkovi* (Khalfina) and to *Syringostromella* cf. *labyrinthia* Stearn by Webby, Stearn & Zhen (1993).

FIG. 35. A-H, *Amphipora ramosa* (Phillips, 1841). A, JCUF11469, longitudinal section, × 5; B, JCUF11472, transverse section, × 3; C, JCUF11475 transverse section, × 3; D, JCUF11769, transverse section, × 3; E, JCUF11475, longitudinal section, × 3; F, JCUF11469, transverse section (oblique), × 3; G, JCUF11475, transverse section, × 30; H, JCUF11469, longitudinal section, × 25. I-Q, *Amphipora pervesiculata* Lecompte, 1952; I, JCUF11460, longitudinal section, × 5; J, JCUF11461, longitudinal section, × 5; K, JCUF11460, longitudinal section, × 5; L, JCUF11447, longitudinal section, × 5; M, JCUF11460, transverse section, × 5; N, JCUF11447, transverse section, × 5; O, JCUF11462, transverse section, × 16; P, JCUF11460, longitudinal section and transverse section, × 7; Q, JCUF11447, longitudinal section, × 15.

Stromatopora sp.
(Fig. 41)

MATERIAL. JCUF12025-28, 12054-6, 12058. All are from JCUL788.

DESCRIPTION. Medium domical skeleton up to 10cm wide and 6cm high; terminal surface not preserved, but strongly undulating coenostromes suggest well developed mamelons. Skeleton with crude latilaminae 5-15mm apart. Astrorhizae poorly preserved. In vertical section skeletal network variable, ranging from a cassiculate network to zones where vertical elements are more prominent. Coenosteles relatively short, commonly oblique, but where longer persist for up to 3 coenostromes high, 7-8 per 2mm, relatively thin (0.05-0.10mm) and coarsely cellular or melanospheric. Coenostromes shorter, impersistent, more often oblique, forming a classic cassiculate network, 6-8 per 2mm and 0.05-0.10mm thick. Galleries rounded or slightly higher than wide. Rare, gently arcuate dissepiments cross the higher galleries. In tangential section galleries rounded to shortly vermiform, and the skeletal structure is relatively closed. In both LS and TS common, much thicker astrorhizal canals are present. They are irregular
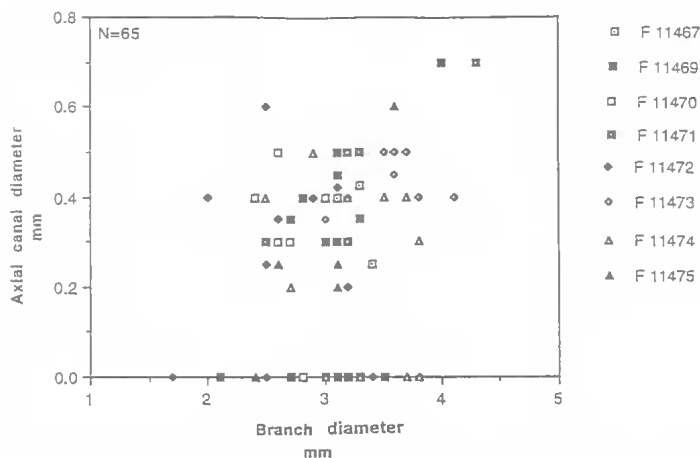

FIG. 36. Branch diameter plotted against axial canal diameter for *Amphipora ramosa* (Phillips, 1841) from the Burdekin Formation.

and suggest a complex, large canal system. No dissepiments preserved in these canals.

REMARKS. The material is confidently assigned to *Stromatopora* on the basis of the cellular skeletal elements which form a cassiculate network. It differs from Burdekin *S. huepschii* by the finer skeletal network, and thinner elements. Burdekin material assigned to *Salairella* cf. *S. cooperi* has a much more closed and slightly more ordered skeletal network. Limited material prevents specific assignment.
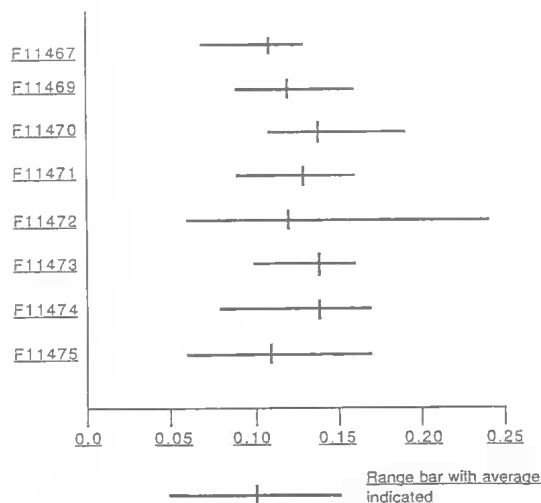
Ferestromatopora Yavorsky, 1955

Ferestromatopora Yavorsky 1955,: 109; Galloway 1957: 446; Stearn 1966a: 111; Stearn 1980: 892; Bogoyavlenskaya & Khromych 1985: 76; Stock, St. Jean & Otte 1990: 4; Stearn 1993: 212.
Not *Ferestromatopora* Yavorsky , Galloway1960: 627; Stearn 1966b: 57; Birkhead 1967: 66; Khromych 1976: 63.
In part *Ferestromatopora* Yavorsky , Fischhuch 1969: 175; Kazmierczak 1971: 96; Khromych 1974: 52; Yang & Dong 1979: 56.

TYPE SPECIES. *Ferestromatopora krupennikovi* Yavorsky 1955 from the Middle Devonian of the Kuznets Basin, Tyrgan region, Russia by subsequent designation of Galloway (1957: 446) being the first species described.

DISTRIBUTION AND AGE. Australia, Givetian; Russia Givetian; Poland, Givetian; Canada, Frasnian; China, Givetian.

REMARKS. In a recent review Stearn (1993) has narrowed the generic concept considerably to 4,

FIG. 37. Ratio of axial canal diameter to branch diameter for *Amphipora ramosa* (Phillips, 1841) from the Burdekin Formation.

or possibly 5 species. Further comment is unnecessary.

Ferestromatopora heideckeri
sp. nov.
(Figs 42, 43).

ETYMOLOGY. For Dr E.J. Heidecker, University of Queensland, Brisbane Australia, for his contributions to palaeontologic and other studies of the Burdekin Subprovince.

MATERIAL. HOLOTYPE: JCUF-11983 PARATYPES: JCUF11986, 89, 93. Additional material 11984-12002, 12022 (less holotype and paratype specimens). All from JCUL788.

DIAGNOSIS. *Ferestromatopora* with paralaminae spaced 0.3mm to 2.2m apart, separating a network of sub-vertically oblique thin skeletal elements (coenosteles) 0 05-0.10mm thick, spaced 7-11 in 2mm and somewhat subordinate sub-horizontally oblique elements spaced 8-12 per 2mm, which are 0.05-0.10mm thick.

DESCRIPTION. Skeletal shape medium domical, up to 8.5cm high and 12.0cm wide; mostly known from fragmental material. Latilaminae (paralaminae sets) seen in only thin section. Growth surfaces gently undulose to flat without obvious mamelons or prominent astrorhizae. In vertical section the skeleton is

FIG. 39. Ratio of axial canal diameter to branch diameter for *Amphipora pervesiculata* Lecompte, 1952 from the Burdekin Formation.
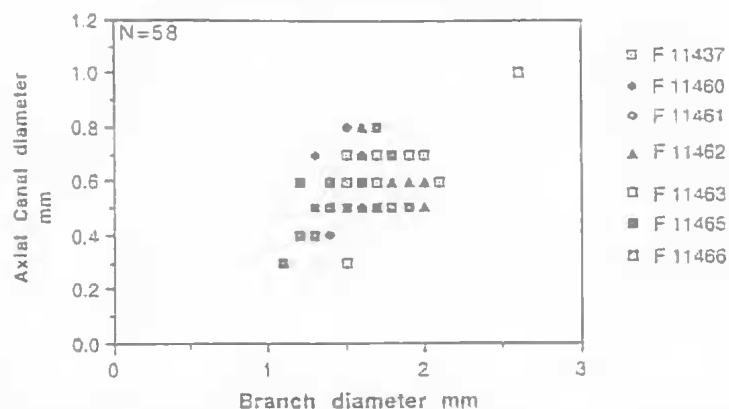

FIG. 38. Branch diameter plotted against axial canal diameter for *Amphipora pervesiculata* Lecompte, 1952 from the Burdekin Formation.

dominated by skeletal network sets separated by continuous, thin compact, laminae or paralaminae (*sensu* Stearn, 1993). The spacing of the paralaminae varies from 0.3mm (1-2 coenostroms) to 2.2mm (7-13 coenostroms) in thickness. Between these laminae thin skeletal elements form a disordered network. Elements short, mostly oblique but dominated by those oriented sub-vertically rather than sub-horizontally. These sub-vertical coenosteles are spaced 7-11 per 2mm and are 0.05 to 0.10mm thick. Sub-horizontal elements (coenostroms) are generally a little shorter, spaced 8-12 per 2mm and are also 0.05-0.10mm thick. They appear subordinate to the sub-vertical elements. Galleries small, mostly rounded and slightly vertically elongate, but they do not extend vertically beyond one coenostrom in thickness. Dissepiments are rare. In tangential section the skeletal elements form an enclosed to labyrinthine structure with galleries vermiform, ovoid or rounded. The microstructure of the skeleton is not well preserved.

In some parts of vertical section, elements which are diffusely melanospheric with fine-grained dark spots are locally adjacent to elements which appear extremely coarsely melanospheric with one or 2 dark spots per element. The laminae are exclusively compact. In tangential section there is sporadic weak development of astrorhizae, consisting of simple, short, walled, and unbranched canals without dissepiments.

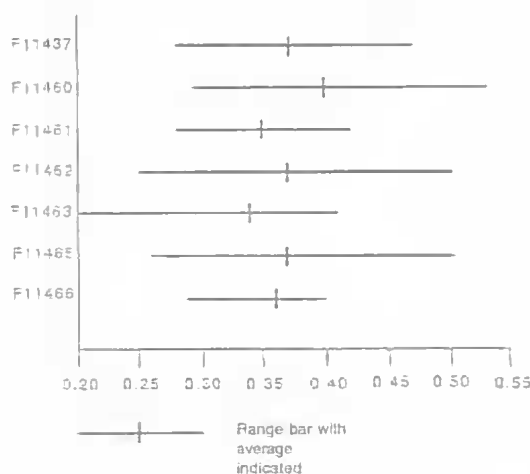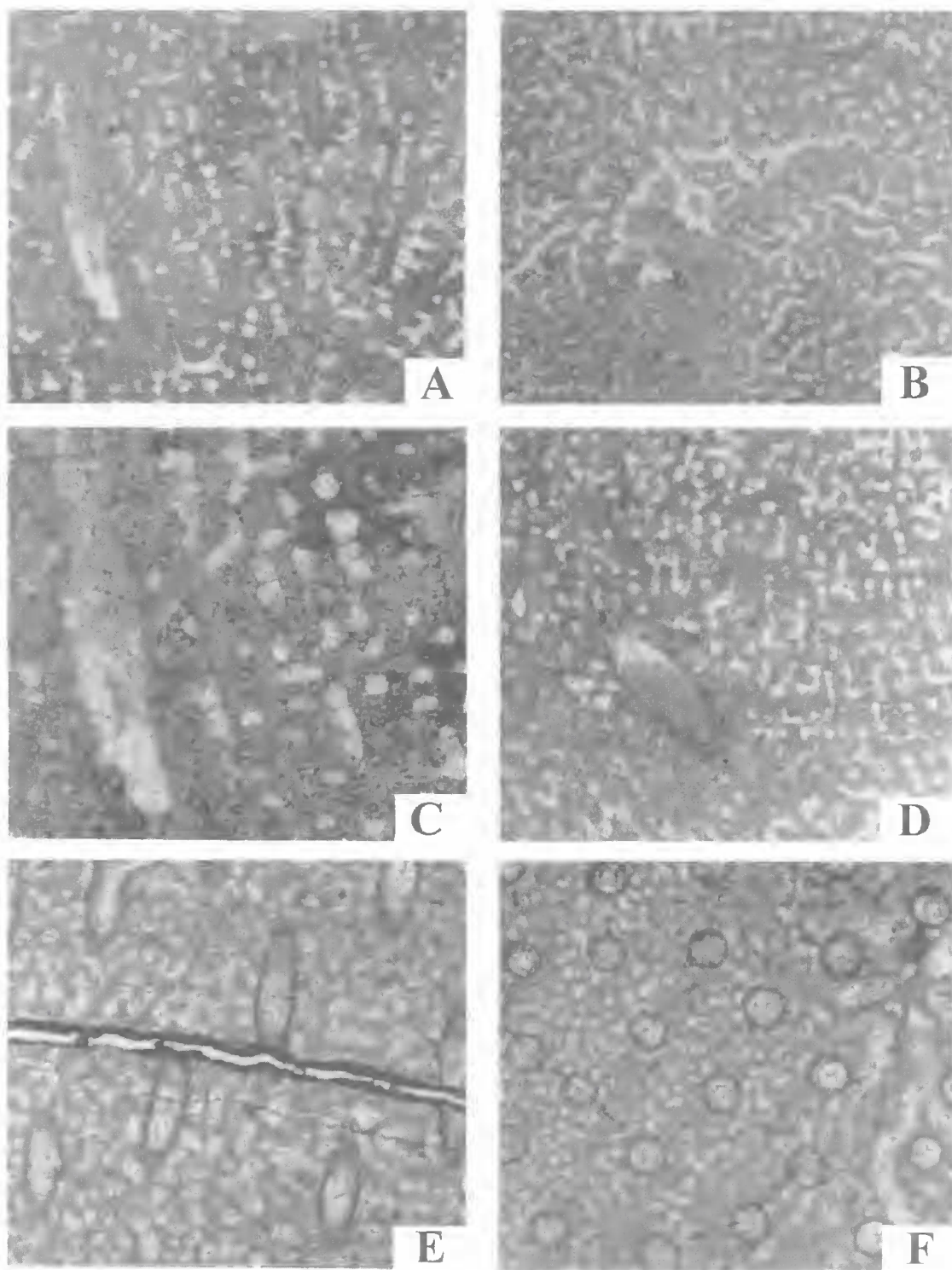DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Middle Devonian.

FIG. 40. *Stromatopora huepschi* (Burgatzky, 1881a). A-C, JCUF11722. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D, JCUF11755 vertical section × 10. E, F, JCUF11931. E, vertical section × 10; F, tangential section × 10.

REMARKS. Paralaminae separating the network packages of oblique elements and, the absence of coenotubes place this material within the generic concept as recently reviewed by Stearn (1993). Yavorksy's (1955) illustrations of the type species *F. krupennikovi* Yavorsky, show somewhat more regularly spaced paralaminae and the network elements are less vertical in aspect. *F. talovensis* Yavorsky has closer-spaced laminae and more reclined elements. *F. tyrganensis* Yavorsky has thicker and obviously more reclined network elements. *F. formosa* Yang & Dong has more closely spaced paralaminae, and thicker interlaminar elements. This new taxon is differentiated on the basis of the thinner sub-vertical, more steeply inclined elements, and the spacing of the paralaminae.

Pseudotrupetostroma
Khalfina & Yavorsky, 1971

TYPE SPECIES. *Stromatopora pellucida* var. *artyschtensis* Yavorsky, 1955.

Pseudotrupetostroma ambiguum
(Cockbain, 1984)
(Fig. 44)

Hermatostroma ambiguum Cockbain 1984: 26, pl. 13a-d.

MATERIAL. JCUF12754-7, all from Fanning River, JCUL788.

DESCRIPTION. Medium domical skeleton up to 7.5cm thick and 25.0cm wide, strongly latilaminate, with thicknesses of approximately 0.5-2.0cm. Growth surfaces gently undulose, forming enveloping surfaces. Astrorhizal traces common but obscure in hand specimen. Mamelons inferred by sporadic rises in growth surfaces. In vertical section coenosteles and coenostromes form an imperfect, closed, grid network in which coenosteles dominate. Coenosteles 5-7 per 2mm, 0.15-0.22mm thick, continuous, superposed through many coenostromes and slightly spool shaped in interlaminar space. Where preserved they show peripheral membranes. Coenostromes less continuous, 6-8 per 2mm, and are highly variable in thickness (0.05-0.22mm), commonly replaced by thin compact dissepiments, locally forming microlaminae. Coenostromes tripartite with a thin light or dark central line, dividing upper and lower divisions of skeletal material. Peripheral membranes extend onto coenostromal surfaces. Skeletal elements compact, including peripheral membranes and dissepiments. Galleries rounded
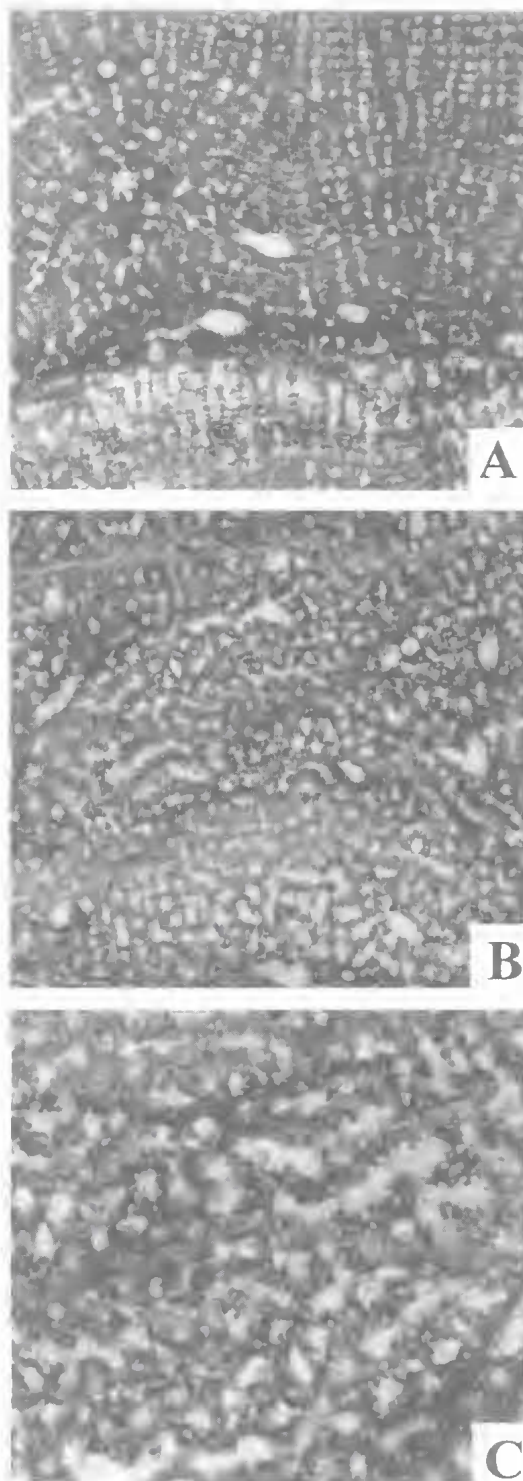

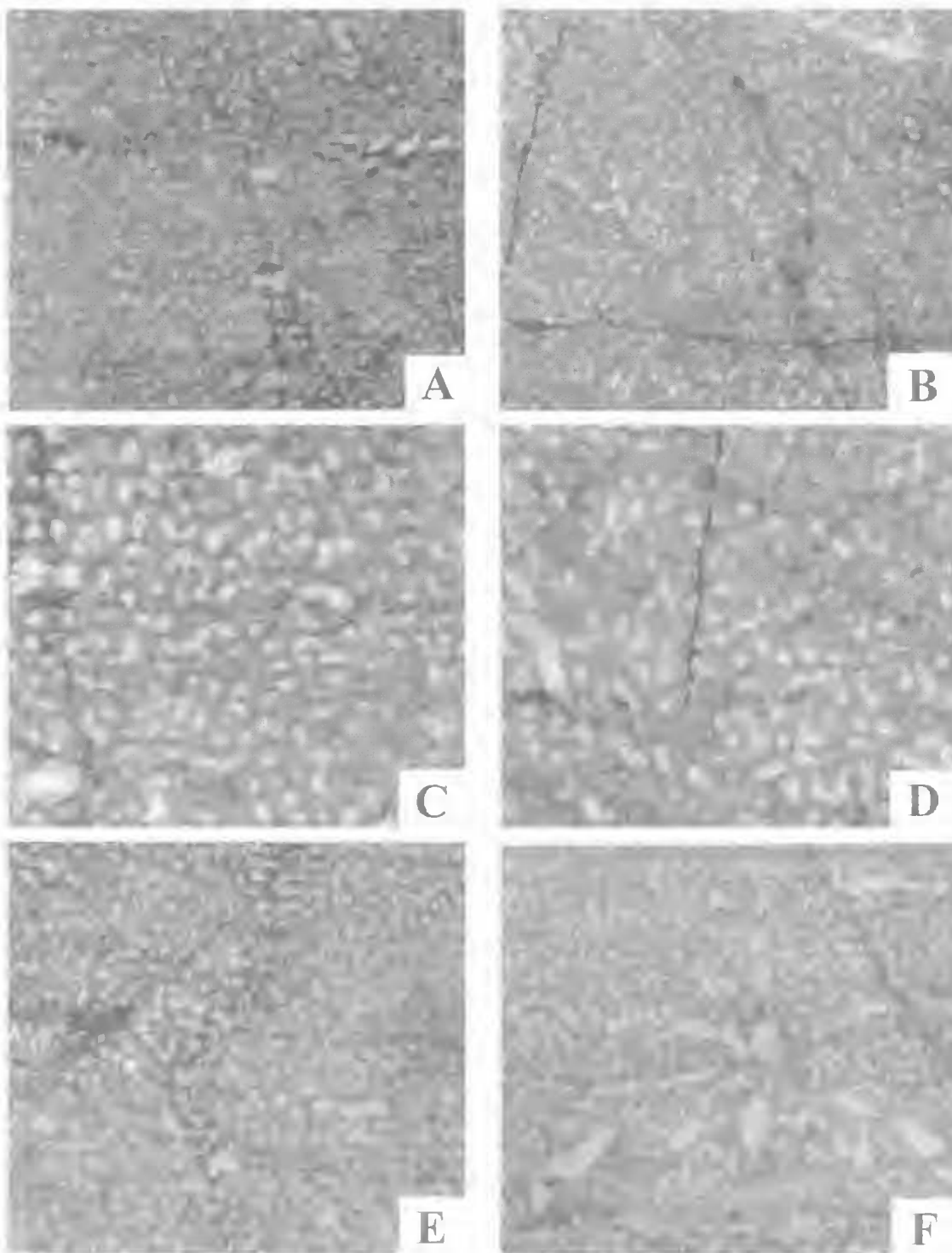FIG. 41. *Stromatopora* sp. JCUF12028. A, vertical section × 10; B, tangential section × 10; C, tangential section × 20.

FIG. 42. *Ferestromatopora heideckeri* sp. nov. A-D, holotype JCUF11983. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E,F, paratype JCUF11989. E, vertical section × 10; F, tangential section × 10.

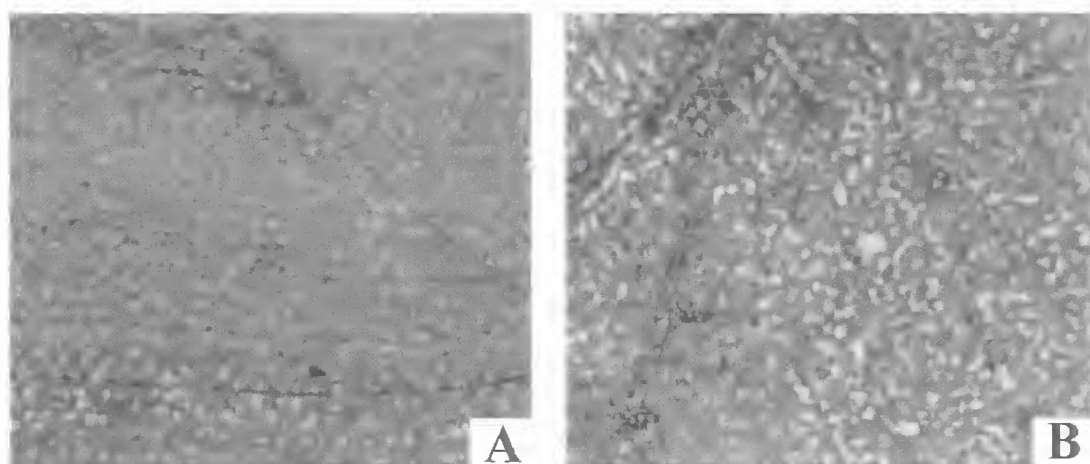FIG. 43. *Ferestromatopora heideckeri* sp. nov. paratype JCUF11986. A, vertical section × 10; B, tangential section × 10.

in vertical section, some vertically elongate, commonly crossed by dissepiments. Astrorhizal canals wide, containing many strongly arcuate dissepiments. In tangential section skeletal elements form a closed labyrinthine network. Galleries rounded to vermiform and show, where preserved, abundant peripheral membranes. Gallery dissepiments uncommonly seen in tangential section. Astrorhizal canals walled, commonly crossed by disspeiments and form simply branched systems.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian; Canning Basin, Western Australia, Late Devonian, Frasnian.

REMARKS. The peripheral membranes, the grid-like skeletal structure, and the tripartite laminae immediately suggest this material as *Hermatostroma*. Examination of paratype material of *H. ambiguum* Cockbain, from the Canning Basin, in particular GSWA10430, has shown it to be indistinguishable from the Burdekin material. The dominance of coenosteles and the reduction of coenostromes to dissepiments in places indicates the species is better placed within *Pseudotrupetostroma*, althought the tripartite coenostromes, peripheral membranes and spool shaped coenosteles in inter-coenostromal space are problematic.

Salairella Khalfina, 1960

Salairella Khalfina 1960: 330; Lessovaya 1970: 88; Yang & Dong 1979: 58; Stearn 1980: 892; Stearn 1983: 555; Mistiaen 1985: 145; Bogoyavlenskaya & Khromych 1985: 87; Stearn 1993: 219.

TYPE SPECIES. *Salairella multicea* Khalfina, 1961:331, pl. D-5 fig 3. from the Eifelian of Salair, Russian Federation, by original designation.

DISTRIBUTION AND AGE. Victoria, Australia, Lochkovian-Pragian; Ellesmere Island, Arctic Canada, Early Devonian, Emsian; Middle Devonian: Buchel District, Germany, Middle Devonian; England, Middle Devonian; Salair, Russia, Middle Devonian; Omulveski Mountains, Siberia Middle Devonian; Givetian: Afghanistan, Givetian; Dinant Basin, Belgium, Givetian, Guangxi, China, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. According to Stearn (1983, 1993), *Salairella* is distinguished from *Stromatopora* on the basis of the regular long coenosteles and the characteristic round, enclosed coenotubes in tangential section. The microstructure is akin to *Stromatopora*, quite unlike the unique microstructure of *Parallelopora* (Stearn, 1980, 1983, 1993).

Salairella has been variously placed in the Syringostromellidae by Stearn (1980, 1983) and Dong (1988), in the Stromatoporidae by Khalfina (1960), and in the Yavorskiinidae by Khalfina and Yavorsky (1969), and Dong & Song (1992). The persistence of coenosteles and preponderance of long coenotubes relates well to the Syringostromellidae.

Salairella buecheliensis (Bargatzky, 1881a)
(Fig. 45)

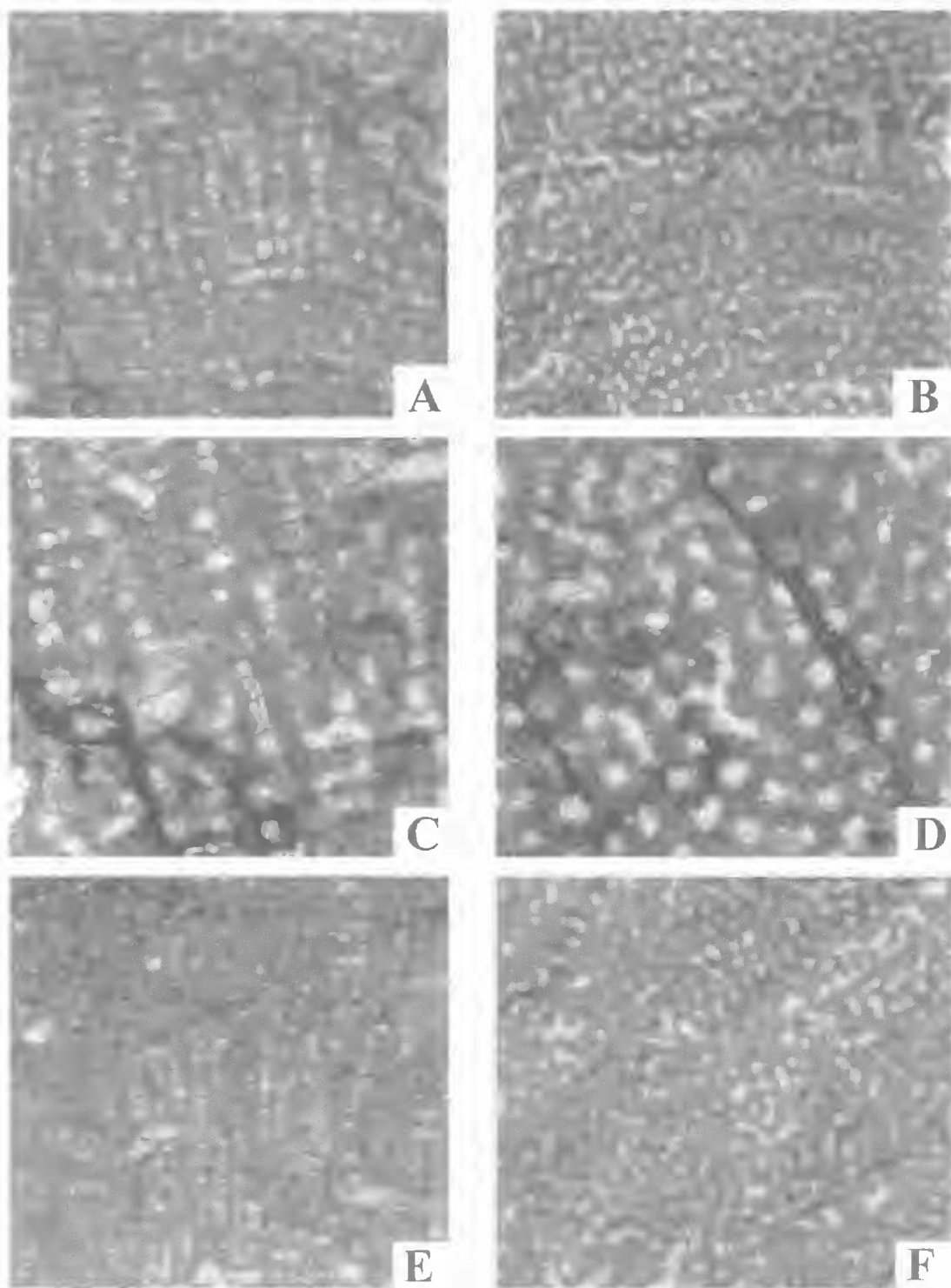*Caunopora bücheliensis* Bargatzky 1881a: 62; Flügel & Flügel-Kahler 1968: 53. (with complete synonymy pre 1968).

FIG. 44. *Pseudotrupetostroma ambiguum* (Cockbain, 1984). A-D, JCUF12754. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D. tangential section × 20. E, F, JCUF12756. E, vertical section × 10; F, tangential section × 10.

Stromatopora bücheliensis (Bargatzky), Nicholson 1886b p. 23, pl. 10, figs. 5-7.
Not *Stromatopora bücheliensis* (Bargatzky), Ripper 1937b; 187, pl. 8, figs. 9-10; Ripper 1937c; 5; Ripper 1938 p. 236.
Parallelopora bücheliensis (Bargatzky), Lecompte 1952; 290.
Salairella buecheliensis (Bargatzky), Mistiaen 1985 p. 145, pl. 12, figs. 10-12, pl. 13, fig. 1.

MATERIAL. JCUF11774, 11776, 11778, 11781, 11792, 11794, 11795, 11796 and 11804 from JCUL788; JCUF11875 from JCUL787; JCUF11903 from JCUL782.

DESCRIPTION. Skeletal shape low domical, small bulbous or irregular. Long coenosteles, 9-14 in 5mm (mean = 10.2,) relatively thick (0.2-0.3mm, mean = 0.23mm), dominate the skeletal structure. Shorter and thinner coenostroms, 0.08 -018 mm thick, often replaced by dissepiments which locally form microlaminae a few coenosteles wide. The galleries approach coenotubes (pseudozooidal tubes) in proportion. In tangential section galleries much reduced, and rounded to vermiform in cross section. Microstructure is melanospheric.

REMARKS. Placement of this species within the genus *Salairella* Khalfina is justified on the basis of microstructure, the long coenosteles and the rounded, reduced galleries in tangential section (Mistiaen 1985). The reduction of the galleries is substantially less in *S. buecheliensis* than in the type species *Salairella multicea* Khalfina. Mistiaen (1985) assigned *Caunopora bücheliensis* Bargatzky (=*Parallelopora bücheliensis* (Bargatzky) of Lecompte, 1952) to *Salairella* Khalfina, on the basis of the microstructure, the dominance of long coenosteles and the diminution of the galleries in tangential section.

Salairella cf. S. cooperi (Lecompte, 1952)
(Fig. 46)

MATERIAL. JCUF12029-34, ?JCUF12035, ?JCUF12036 from JCUL788.

DESCRIPTION. Specimens fragmental, derived from medium domical skeletons up to 13cm wide and 8cm high and not obviously latilaminate in hand specimen. In vertical section, thickened coenosteles dominate a dense skeletal network which occupies up to 70 % of the skeleton. Latilaminae, 1.5-5.0mm thick visible in thin section. Coenosteles long, commonly oblique, persisting up to 5 coenostromal thicknesses, closely spaced (10-16 per 2mm) and thick

(0.15-0.22mm). Coenostromes short, oblique and subordinate to coenosteles, irregularly spaced making measurement of spacing difficult. Coenostromes thick, 0.08-0.12mm. Skeletal elements finely cellular or melanospheric. Galleries very small, rounded, commonly slightly vertically elongate. Dissepiments uncommon. In tangential section the skeletal network is dense and gallery spaces are substantially reduced; vermiform or rounded. Astrorhizae consist of simply branched walled canals, with few dissepiments.

DISTRIBUTION AND AGE. Germany, Middle Devonian; England, Middle Devonian; Dinant Basin, Belgium, Givetian; Afghanistan, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. Lecompte's (1952) illustrations of the holotype of *S. cooperi* show elongate coenosteles, and the characteristic dense skeletal framework. Burdekin material has fewer pillars per 5mm, but the overall structure of the skeleton is consistent with *S. cooperi*. Given the long vertical elements of *S. cooperi*, it is better placed in *Salairella* (see Stearn 1993).

Salairella sp.
(Fig. 47)

MATERIAL. JCUF12024 from JCUL788

DESCRIPTION. Laminar fragment approximately 1.2cm thick and 6.5cm in maximum width, with no obvious latilamination; upper surface silicified. Skeleton contains abundant syringoporid intergrowths, and a subordinate ?vermitid symbiont. In vertical section the structure is dominated by long, thick, persistent coenosteles, 0.15-0.40mm (mean = 0.27mm, σ= 0.06, n=10) thick, spaced 5-7 (n=5) per 2mm. Coenostromes are subordinate, thinner (0.10-0.25mm), and generally impersistent. With vertical elements they form long coenotubal galleries, 0.13-0.30mm wide, crossed by thin, almost flat multitudinous dissepiments. Both coenosteles and coenostromes comprised of medium cellular material; dissepiments are compact. In tangential section skeletal elements dominate, galleries rounded, or less commonly short vermiform. There is a single trace of an astrorhizal canal, which is short, thin, branched dichotomously and crossed by a single dissepiment.
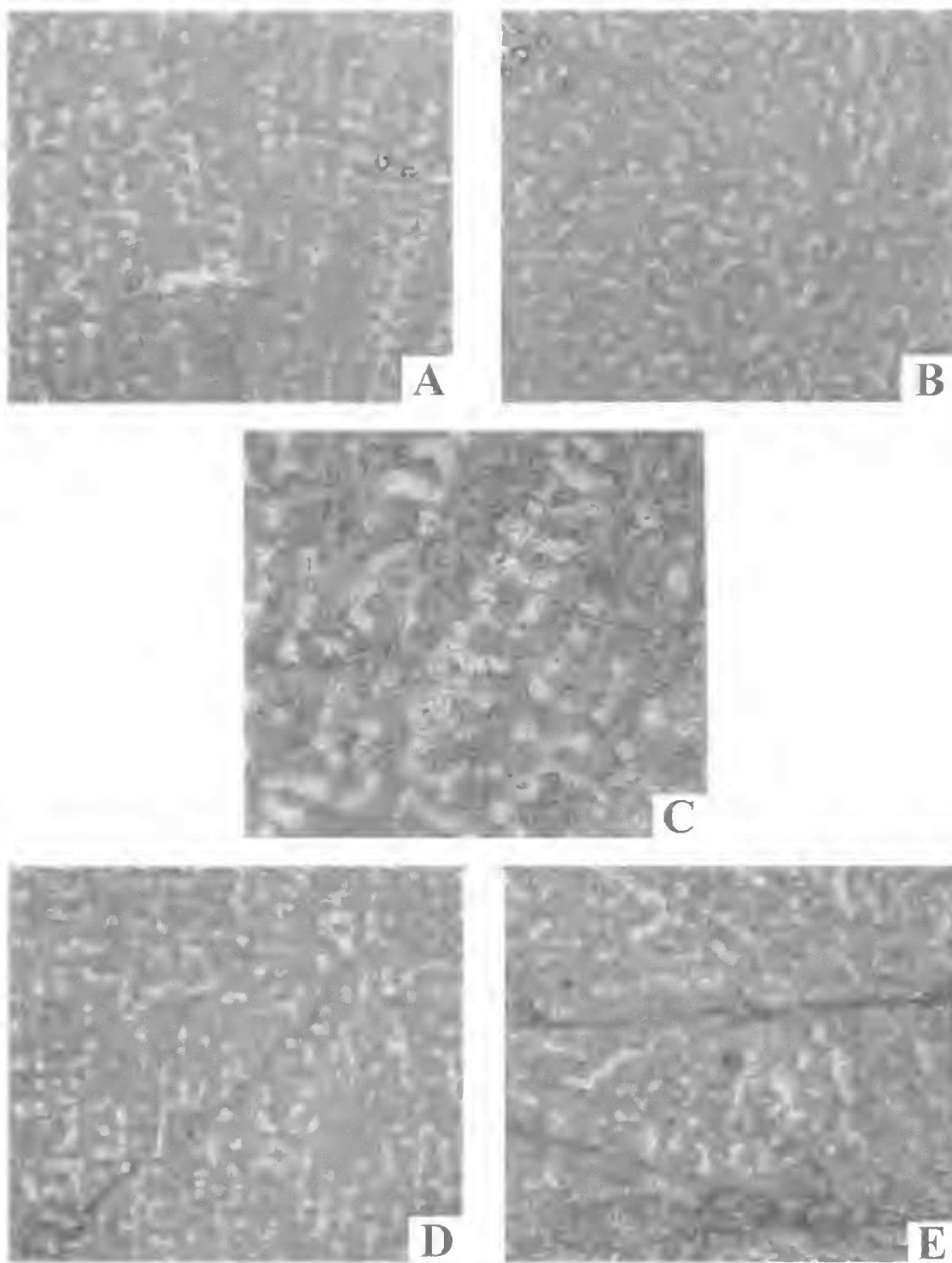
FIG. 45. *Salairella bucheliensis* (Bargatzky, 1881a). A-C, JCUF11776. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20. D,E, JCUF11774. D, vertical section × 10; E, tangential section × 10.
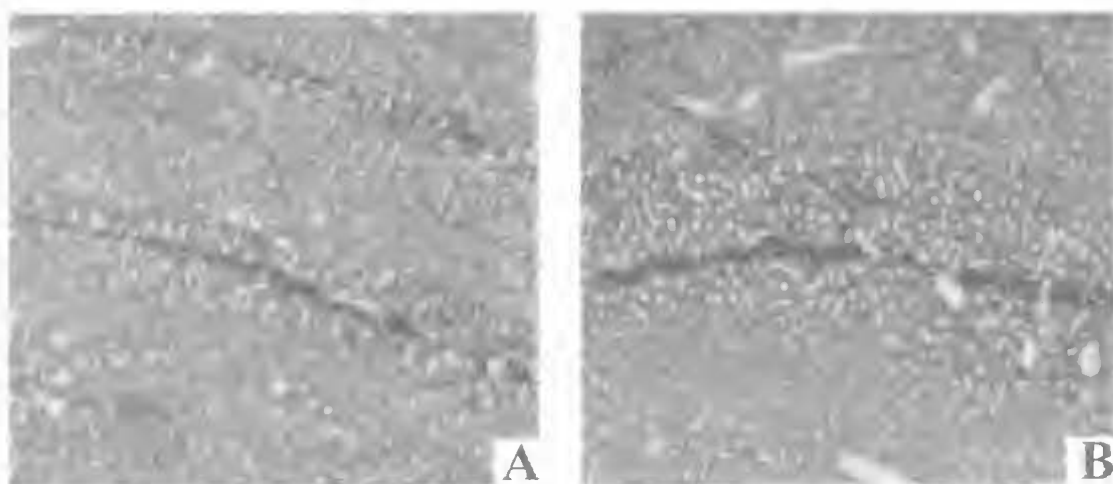
FIG. 46. *Salairella* c.f. *S. cooperi* (Lecompte, 1952) JCUF12034. A, vertical section × 10; B, tangential section × 10.

REMARKS. The occluded rounded galleries and the absolute dominance of vertical elements allies the specimen to *Salairella*. In this respect the specimen approaches the type species, *S. multicea* Khalfina (1961; fig D-5, 3a) but the elements in the Burdekin specimen are much thicker. It is separated from other Burdekin *Salairella* by the vertical element dominance, and the much thickened skeletal elements. More and better preserved material is needed before the species can be named.

Glyptostromoides Stearn, 1983

Glyptostromoides Stearn 1983: 553; Stock, St. Jean and Otte 1990; Stearn 1993: 216.
Glyptostroma Yang & Dong, Bogoyavlenskaya & Khromych 1985: 77; Dong 1988: 32; Stock, St. Jean & Otte 1990: 4.
In part *Glyptostroma* Yang & Dong 1979: 65, 88.
In part *Taleastroma* Galloway, Mistiaen 1985: 148.

TYPE SPECIES. *Glyptostroma simplex* Yang & Dong 1979 from the Middle Devonian (Givetian) of Guangxi, China, by original designation.

DISTRIBUTION AND AGE. Ellesmere Island, Canada, Early Devonian, Emsian;. Afghanistan, Early- Middle Devonian, Emsian to Givetian; Kuznetsk Basin, Russia Middle Devonian, Eifelian; Guangxi, China, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

Glyptostromoides boiarschinovi
(Yavorsky, 1961)
(Fig. 48A,B)

Stromatopora boiarschinovi Yavorsky 1961: 42, pl. 25, figs. 3-5; Khromych & Hung 1988: 24, pl. 10, fig. 2
Glyptostroma boiarschinovi (Yavorsky) Yang & Dong 1979: 67, pl. 36, figs. 5-6
Glyptostromoides boiarschinovi (Yavorsky) Stearn 1983: 553.
Taleastroma boiarschinovi (Yavorsky), Mistiaen 1985 p. 156, pl. 13, figs. 9-10, pl. 14, figs 1-9.
?*Neosyringostroma boiarschinovi* (Yavorsky), Kazmierczak 1971p. 118
Syringostroma? grossum Khromych & Hung 1988: 28, pl. 13, fig. 1.

MATERIAL. JCUF11777 and 11793 from JCUL788; 11782, 11841, and JCUF12021 from JCUL787 .

DESCRIPTION. Skeletal shape laminar to very low domical, up to 27mm high and 120mm wide. Latilaminae are in contact with neighbouring latilaminae, they may be 7-11mm apart. All specimens contain syringoporid and ?vermitid symbionts. Growth surface gently undulose without obvious mamelons. Astrorhizae indistinct. In vertical section skeleton comprised of an irregular network of short, thick, horizontal, vertical and oblique elements which is pierced by widely spaced, long, persistent, thicker coenosteles. Smaller vertical elements (coenosteles) slightly, but not obviously, dominate the irregular network. They are not persistent, only 1-2 coenostromes high. Horizontal elements (coenostroms) discontinuous, thick and subordinate. Oblique elements sporadically arise from the terminations of the short coenosteles and more commonly arise from ends of coenostroms.
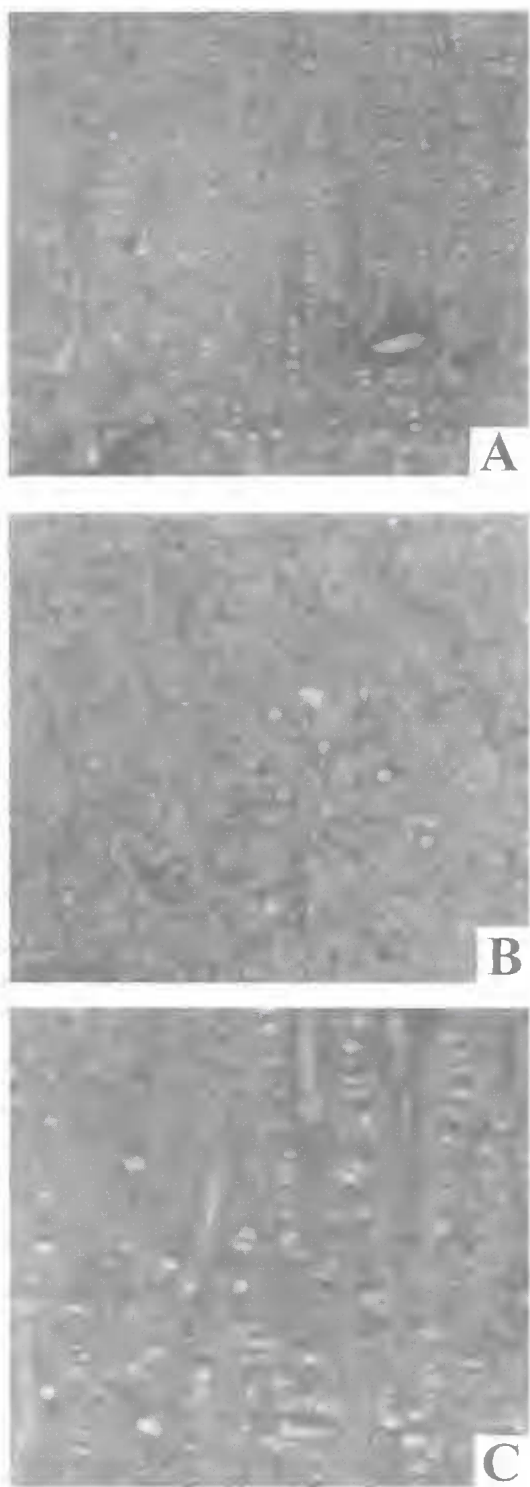
Smaller skeletal elements equally thickened (0.15-0.22mm) consisting of diagenetically modified, now diffusely flocculent microstructure throughout the vertical section, but there are sporadic patches of conspicuously melanospheric (?altered cellular) skeletal material. Longer coenosteles penetrate up to 20 coenostroms, are somewhat thicker than smaller elements (0.22-0.30mm) and consist of sporadically melanospheric material. Long elements rarely show a persistent, dark central line. In tangential section skeletal elements form a labyrinthine network which encloses dominantly vermiform and sporadic circular galleries free of dissepiments. Melanospheric microstructure is obvious. Thicker circular pillars, and poorly connected pillars interpreted as terminations of long coenosteles, rarely show a dark centre. Commensals consists of a fine, thin, dominant syringoporid and a subordinate helically coiled ?vermitid.

DISTRIBUTION AND AGE. Salair, Russia, 'Eifelian' (=Emsian cf. Mistiaen 1985); Holy Cross Mts, Poland, Givetian. Vietnam, Middle Devonian; Guangxi, China, Givetian; Afghanistan, Givetian; Burdekin Subprovince, north Queensland, Australia, Givetian.

REMARKS. The type species *Glyptostromoides simplex* (Yang & Dong, 1979) possesses a much more enclosed network than the Burdekin material. *G. oblique* (Yang & Dong, 1979) has similar widely spaced larger coenosteles and appears to possess microlaminae (Yang & Dong, 1979, pl. 35, fig. 7). *G. luijingensis* (Yang & Dong, 1979) has much more rounded galleries in both vertical and horizontal section. The Burdekin material is conspecific with *Glyptostromoides boiarschinovi* (Yavorsky, 1961) showing a relatively open network, somewhat subdued larger coenosteles and alabyrinthine network. Mistiaen (1985) and Stearn (1993) placed this taxon within *Taleastroma*. This view is not endorsed: pillars are generally not as isolated as in other *Taleastroma* taxa listed by Stearn (1993), nor are the pillars annular (Mistiaen pl. 14, fig. 5 excepted). The larger coenosteles are submerged into the labyrinthine network, and are only rarely identifiable in tangential section. This species does show, however, a more open network than other *Glyptostromoides*. Placement in *Syringostromella* is precluded by the the lack of a truly open network of galleries in tangential section (Stearn, 1993).
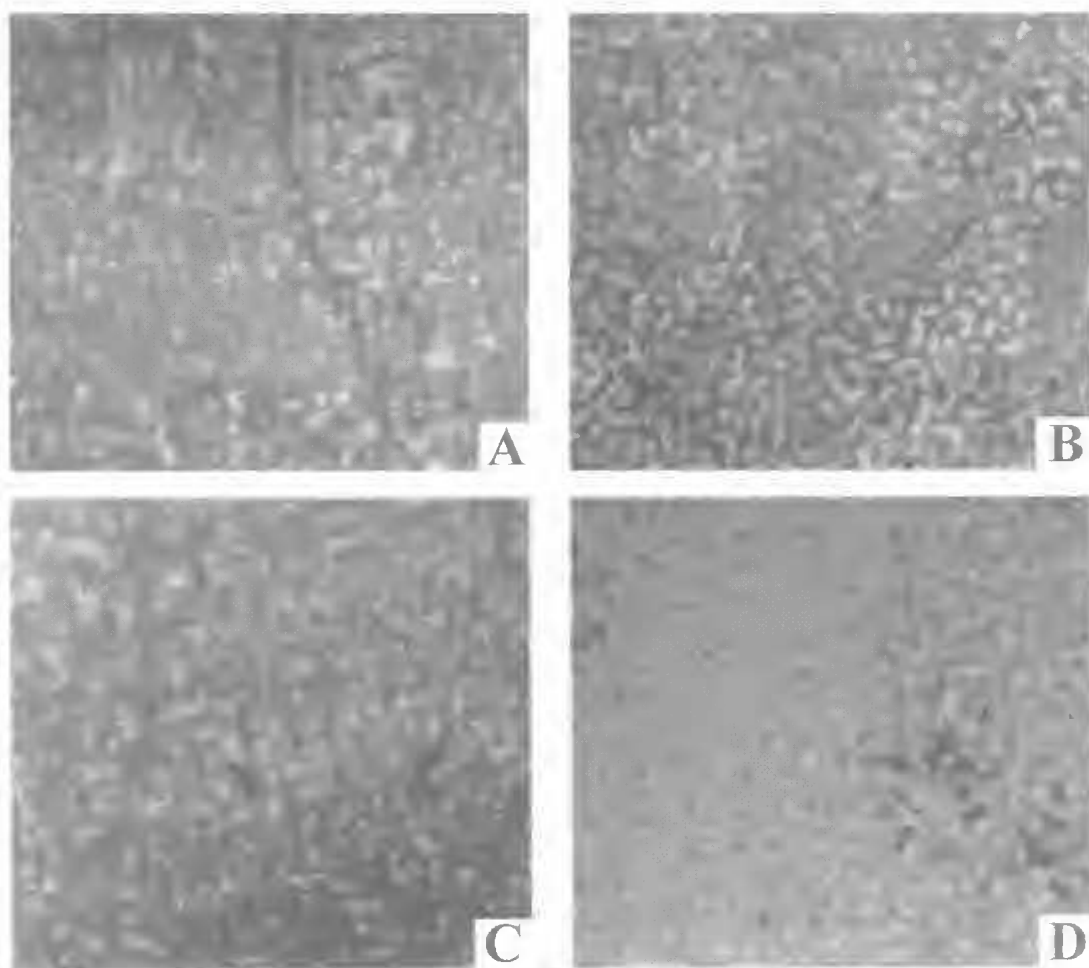
FIG. 47. *Salairella* sp. JUF12024. A, vertical section × 10. B, tangential section × 10. C, vertical section × 20.

FIG. 48. A, B, *Glyptostromoides boiarschinovi* (Yavorsky, 1961), JCUF11841. A, vertical section × 10; B, tangential section × 10. C, D, *Taleastroma* sp. JCUF12023. C, vertical section × 10; D, tangential section × 10.

Taleastroma Galloway, 1957

Taleastroma Galloway 1957: 65; Stearn 1966a: 112; Flügel & Flügel-Kahler 1968: 578; Yang & Dong 1979: 60; Stearn 1980: 892; Bogoyavlenskaya & Khromych 1985: 91; Stock, St. Jean, & Otte 1990: 8; Stearn 1993: 215.
?In part *Neosyringostroma* Kazmierczak 1971 p. 117.
In Part *Glyptostroma* Yang & Dong 1979 p. 65.

TYPE SPECIES. *Stromatopora cummingsi* Galloway & St. Jean by subsequent designation, from the Middle Devonian Logansport Limestone, Indiana.

DISTRIBUTION AND AGE. Australia, Givetian; Guangxi, Givetian, Guiezhou, China, Givetian; Afghanistan, Emsian; Indiana, United States, Middle Devonian; Belgium; Eifelian; Holy Cross Mountains, Poland, Middle Devonian.

REMARKS. Recent reviews of *Taleastroma* have been given by Mistiaen (1985) and by Stearn (1993) who has clarified the previously problematic concept of this genus. *Taleastroma* is separated from *Glyptostromoides* by the rounded pillars in tangential section, the compact axial zones of the large pillars, and the columnar pillars which are well differentiated from the cassiculate network. *T. pachytextum* of Turnsek (1970) does not represent *Taleastroma*; as it has no well developed cassiculate structure and vertical elements are overwhelmingly dominant. Stearn's (1993) assignment of *G. boiarschinovi* Yavorsky to *Taleastroma* is not accepted, as discussed previously.
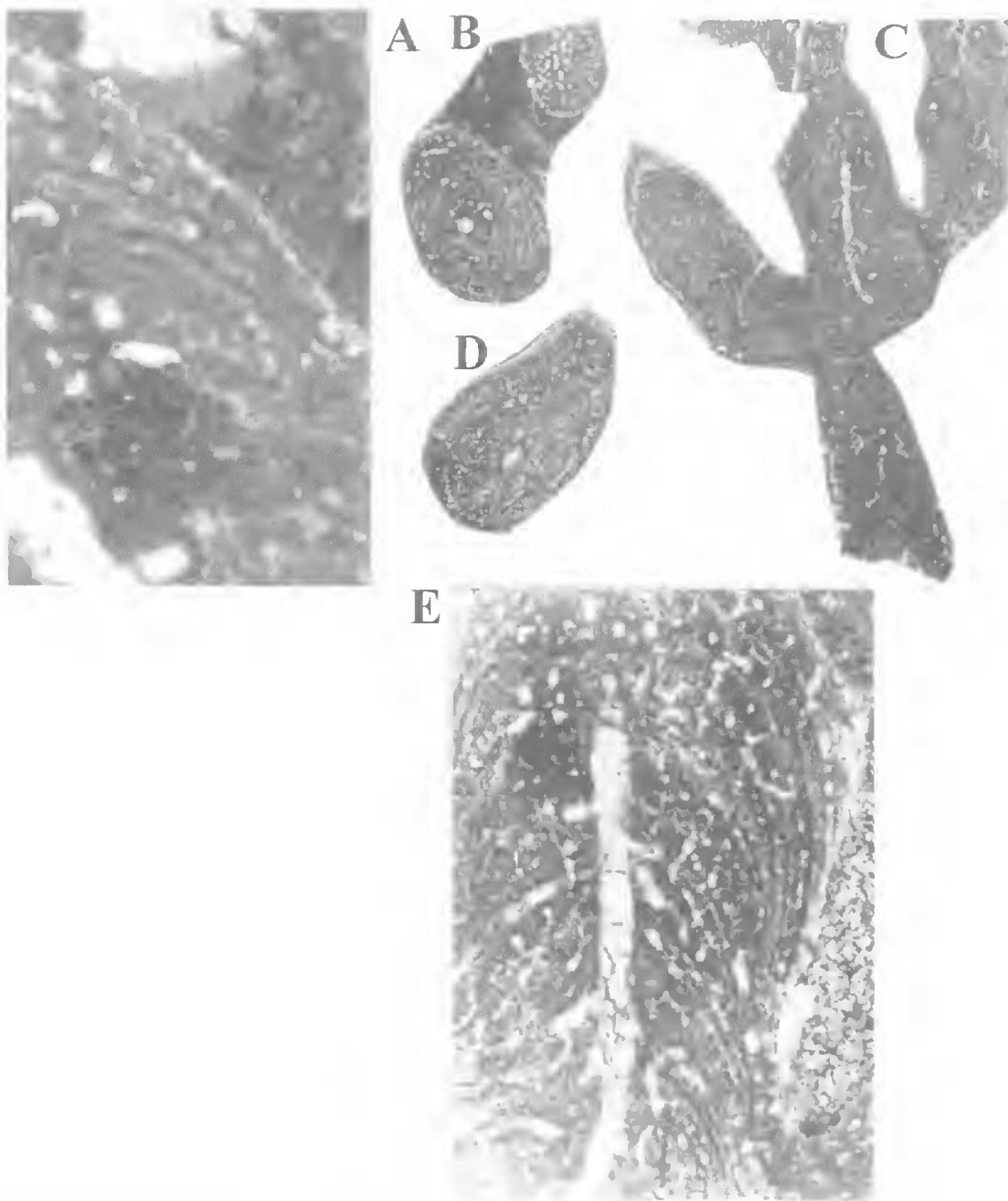
FIG. 49. A-E. *Stachyodes crassa* (Lecompte, 1952). A, JCUF11392, longitudinal section, × 25; B, JCU11393, transverse section, × 3; JCUF11392, longitudinal section, × 2; D, JCUF11291, transverse secton, × 2; E, JCUF11392, longitudinal section, × 6.

Taleastroma sp.
(Fig. 48C,D)

MATERIAL. JCUF12023 from JCUL788.

DESCRIPTION. Single fragment of a medium domical skeleton, with rare auloporid intergrowths. In vertical section the specimen shows only partial preservation of its original

skeleton. Moderately long, continuous pillars, 12-16 per 5mm, with conspicuous dark axes and coarsely cellular peripheries, 0.18-0.30mm thick (axis ranging from 0.08-0.15mm). Pillars dominate a disordered network of oblique to horizontal elements which are coarsely cellular, highly variable in thickness (0.08-0.25mm) and have no regular spacing. Gallery spaces irregular to rounded, with no obvious dissepiments. In tangential section the specimen is very poorly preserved. However moderately isolated pillars can be discerned.

REMARKS. The dark-centred, long pillars, dominating an essentially cassiculate network, and appearing isolated in tangential section allow confident assignment to *Taleastroma* Galloway. Lack of material and the indifferent preservation prevents specific assignment.
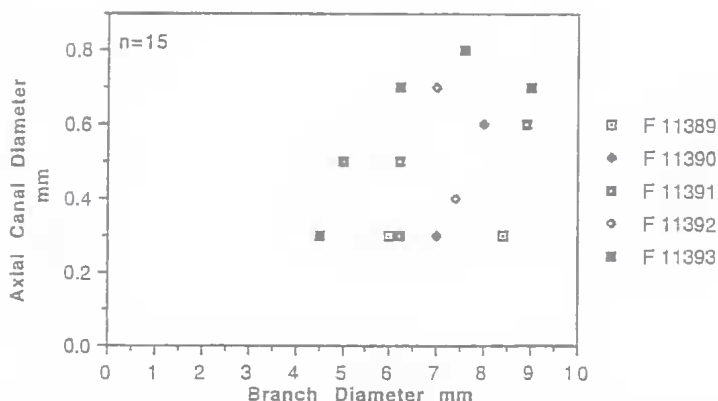

FIG. 50. Branch diameter plotted against axial canal diameter for *Stachyodes crassa* (Lecompte, 1952) from the Burdekin Formation. In this and subsequent morphometric data sets; Dx = mean branch diameter (mm), Dó = standard deviation. Ax = mean axial canal diameter (mm), As = standard deviation and n = number of branches or axial canals measured in slide.

SYRINGOSTROMATIDA Bogoyavlenskaya, 1969
STACHYODITIDAE Khromych, 1976

Stachyodes Bargatzky, 1881b

Stachyodes Bargatzky 1881b: 688; Nicholson 1886: 107; Pocta 1894: 138; Heinrich 1914: 38 (Translated Lcverne, 1916: 58); Kuhn 1927: 547; Lecompte 1952: 298; Lecomptc 1956: F136; Galloway 1957: 444; Yavorsky 1957: 58; Gogolczyk 1959: 360, 380; Galloway & Ehlers 1960: 101; Yavorsky 1961: 53; Stcarn 1962: 8; Stearn 1963: 660; Yavorsky 1963: 76; Klovan 1966: 31; Stearn 1966: 116; Birkhead 1967: 85; Yavorsky 1967: 32; Flügel & Flügel-Kahler 1968: 565; Stearn & Mehrotra 1970: 17; Turnsek 1970: 24; Zukalová 1971; 96; Flügel 1974: 178; Khromych 1974: 61; Riding 1974: 572; Stearn 1975b: 1663; Khromych 1976: 68; Yang & Dong 1979: 87; Bogoyavlenskaya 1980: 8; Mistiaen 1980: 217; Stearn 1980: 892; Dong 1982a: 109; Stock 1982: 675; Dong & Wang 1984: 268; Cockbain 1984: 28; Bogoyavlenskaya & Khromych 1985: 88; Mistiaen 1985: 192; Dong 1988: 33; Mistiaen 1988: 183; Dong 1989: 174; Stock, St Jean & Otte 1990: 8; Stearn and Shah 1990: 1742.
Sphaerostroma Gurich 1896: 126.
Keega Wray 1967: 16.
(?)*Stachyodes* Fagerstrom 1982: 43.

TYPE SPECIES. *Stromatopora (Caunopora) verticillata* Mc Coy, 1851. The genus was erected by Bargatzky (1881b) based on *S. ramosa* from Paffrath, Germany but there has been considerable debate over the identity of the type species. Nicholson (1886b) regarded *S. ramosa* Bargatzky as synonymous with *Stromatopora (Caunopora) verticillata* Mc Coy, 1851.

DISTRIBUTION AND AGE. Worldwide, Eifelian to Frasnian.

Stachyodes crassa (Lecompte, 1952)
(Fig. 49A-E.)

Idiostroma crassum Lecompte 1952: 318, pl. 64, fig. 2: Flügel & Flügel-Kahler 1968:. 112; Khromych & Hung 1988: 33, pl. 15, figs. 2-3.
Stachyodes crassa (Lecompte), Galloway & St. Jean 1957: 248; Cockbain 1984: 30, pls. 20b, 21a-c; Bogoyavlenskaya & Khromych 1985: 14.
Stachyodes (Sphaerostroma) crassa (Lecomptc), Zukalová 1971: 104 pl. 35, fig. 1-3, pl. 37, fig. 6.

MATERIAL. JCUF11389-93 from JCUL778.

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Australia, Givetian; Vietnam, Givetian; Canning Basin, Western Australia, Givetian-Frasnian; Dinant Basin, Belgium, Frasnian; Moravian Karst, Czechoslovakia, Frasnian.

DESCRIPTION. Robustly dendroid (stachyodiform) skeletons which branch irregularly, commonly rising from a surface encrustation. Branch diameter 4.5-9.0mm (mean =6.9 , σ= 1.3, n= 15), bases of branches often coalesced. One, or less commonly more, axial canals. Macrostructure relatively regular,
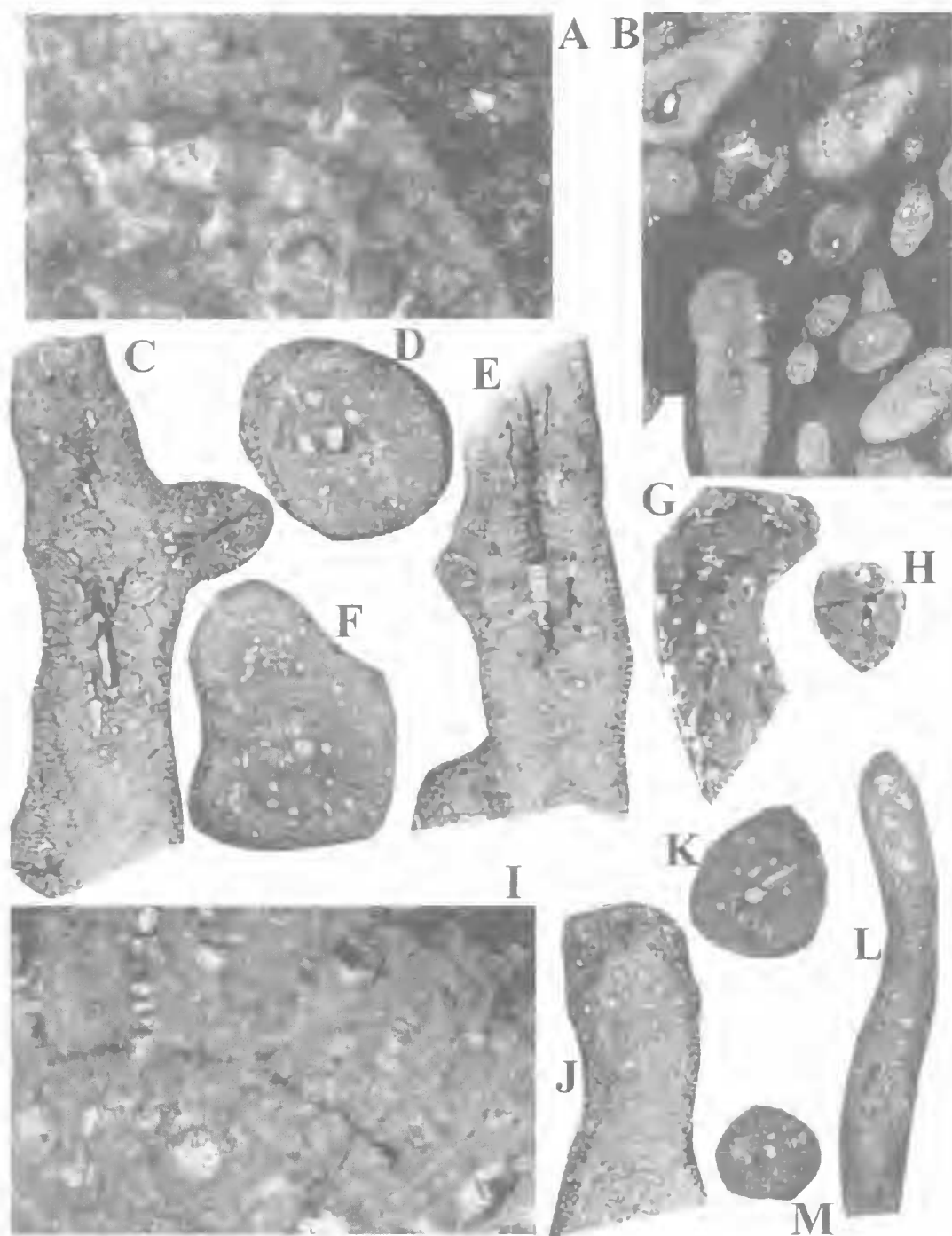
FIG. 51. A-M, *Stachyodes costulata* Lecompte, 1952. A, JCUF11395, longitudial section, ×50; B, JCUF11395, transverse section, × 2; C-F. JCUF11394; C, longitudinal section, × 3; D, transverse section, × 6; E, longitudinal section, × 3; F, transverse section, × 4; G, JCUF11401, longitudinal section, × 2; H, JCUF11401, transverse section, × 2; I, JCUF11394, transverse section, × 50; J, JCUF11394, longitudinal section, × 3; K, JCUF11394, transverse section, × 3; L, JCUF11400, longitudinal section, × 2; M, JCUF11395, transverse section, × 3.

especially at the periphery. Pillars relatively thick, 0.03-0.25mm (mean =0.16mm), and are somewhat superposed. Laminae less distinct than pillars, generally continuous, especially towards periphery, variable in thickness (0.05-0.2mm, mean = 0.12mm). Galleries oval to rounded in transverse section, elongate rounded to rectangular in longitudinal section, 0.15-0.3mm in diameter, and with rare dissepiments. Axial canals are 0.3-0.8mm in diameter (mean = 0.5, σ=0.2, n=15), regularly crossed by dissepiments. Canals intermittently branch along laminae. Microstructure near periphery tangentially (not transversely) fibrous .

MORPHOMETRICS. Morphometric data for the limited number of specimens is summarised below, and a plot of axial canal diameter against skeletal diameter is given in Figure 50.

Specimen	D mean	Dσ	N	A mean	Aσ	n
JCUF11389	7.2	1.2	2	0.3	0.0	2
JCUF11390	7.5	0.5	2	0.45	0.15	2
JCUF11391	6.6	1.4	4	0.5	0.1	4
JCUF11392	6.9	0.5	3	0.5	0.1	3

REMARKS. The species is distinguished by the relatively regular macrostructure in comparison to other species of *Stachyodes*. *S. costulata* is much less regular, tends to be a little smaller in branch diameter, although there is wide, overlapping variation, and has a much more dense skeletal network. Morphometric data are comparable to that given for *S. crassa* by Lecompte (1952), Zukalová (1971) and Cockbain (1984). *Stachyodes crassa* is subordinate in abundance to *S. costulata* within the Burdekin Formation.

<div align="center">

Stachyodes costulata Lecompte, 1952
(Fig. 51)

</div>

Stachyodes costulata Lecompte 1952: 309, pl. 65, figs. 1-4; Gogolczyk 1959: 372, pl. 4, fig. 3, pl. 5, figs. 1-3; Stearn 1963: 660, pl. 86, figs. 4-5; Klovan 1966: 31, pl. 11, figs. 1-6; Yavorsky 1967: 34, pl. 16, figs. 1-4, pl. 16, fig. 7, pl. 18, figs. 1-3; Stearn & Mehrotra 1970: 18, pl. 4, figs.3-4. Khromych 1974: 62, pl. 16, fig. 1, pl. 17, fig. 2; Stearn 1975b: 1663; Fischbuch 1970b: 1079, pl. 148, figs. 5-7; Khromych 1976: 68, pl. 10, fig. 2; Yang & Dong 1979: 87, pl. 9,10; Dong 1982a: 287, pl. 5, figs. 3,4; Dong, 1981: 109, pl. 5, figs. 5-6; Stock, 1982: 676, pl. 4, figs. 7-9; Cockbain 1984: 28, pl. 19a-d, 20a; Bogoyavlenskaya & Khromych 1985: 14; Khromych & Hung 1988: 34, pl. 16, fig. 6; Dong 1989: 174, pl. 2, 3a-d; Stearn & Shah 1990: 1752; Webby & Zhen 1997, 51, fig 19.

Stachyodes cf.*costulata* Lecompte, Yavorsky 1961: 35, pl. 17, figs. 1-6; Yavorsky 1963: 124, figs. 10-12, pl. 25, figs.4-5; Yavorsky 1967: 35, pl. 17, figs. 1-6.
Stachyodes (Stachyodes) costulata Lecompte, Zukalová 1971, p. 101, pl. 34, figs. 5-6.

DISTRIBUTION AND AGE. Burdekin Subprovince Givetian and Broken River Province Givetian to ?Frasnian, north Queensland,; Canning Basin, Western Australia, Frasnian; Dinant Basin, Belgium, Frasnian; Holy Cross Mountains, Poland, Givetian-Frasnian; Italy, Frasnian; Czechoslovakia, Givetian-Frasnian; Timan, Russia, Frasnian; Southern Tianshan, China, Givetian; Sichuan, China, Givetian; Xizang, China, Givetian; Yunnan, China, Givetian-Frasnian; Central and Southern Guangxi, China, Frasnian; Vietnam, Givetian to Frasnian; Canada, Givetian-Frasnian; Iowa, Frasnian.

MATERIAL. JCUF11394, 11396, 11397, 11401 from JCUL788; JCUF11395 from JCUL781; JCUF11403 from JCUL778; JCUF11398 from JCUL784; JCUF11404-11409 from JCUL779.

DESCRIPTION. Robustly dendroid (stachyodiform) skeletons in some cases irregularly rising from an encrustation surface with branches 4.0-9.8 mm (mean =5.8, σ=1.3, n= 27) in diameter. One to 5 axial canals, 0.2-0.8 mm in diameter (mean = 0.4, σ= 0.2, n= 47), regularly crossed by gently arcuate dissepiments. Skeletal material greatly thickened, producing a diminution of galleries which only become obvious at the skeletal margin where they attain diameters of 0.08- 0.18mm and are normal to the surface. Microstructure not easily discernible but is fibrous with striations parallel to the margins of the skeleton.

MORPHOMETRICS. Morphometric data are summarised below and a comparison of skeletal diameters is given in Fig. 52. NC_m= mean number of axial canals per branch.

Specimen	D mean	Dσ	n	A mean	Aσ	n	NCm
JCUF11394	6.2	0.9	11	0.5	0.2	24	2.2
JCUF11396	5.1	-	1	0.3	0.1	5	5.0
JCUF11397	5.3	-	2	0.4	0.1	5	2.5

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NON CANALICULATE FORMS

</div>

Specimen (Dx, n); JCUF11401 (6.5, 3); JCUF11403 (9.8, 1); JCUF11399 (4.8,1).

REMARKS. *S. costulata* is more common within the Burdekin Formation than *S. crassa* and is distinguished by its dense skeletal network. The

Stachyodes costulata

Legend:
- □ F 11394
- ◆ F 11396
- ▣ F 11397
- ○ F 11399
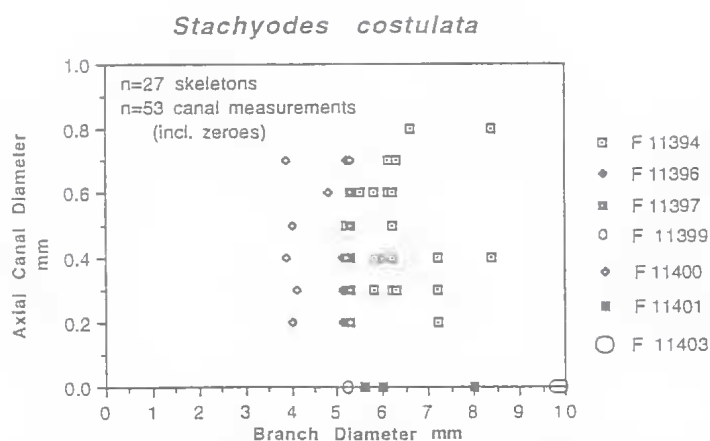- ◇ F 11400
- ■ F 11401
- ○ F 11403

FIG. 52. Branch diameter plotted against axial canal diameter for *Stachyodes costulata* Lecompte, 1952 from the Burdekin Formation.

material compares closely with *S. costulata* of Lecompte (1952), Zukalová (1971) and Cockbain (1984). *Stachyodes costulata* Lecompte from the Stanley Limestone Member, in the Broken River Province of Webby & Zhen (1997) are indistinguishable from the Burdekin material. The species is distinguished from *S. crassa* on the basis of a much less regular network of skeletal elements. It differs in branch diameter from *Stachyodes* sp. A and *Stachyodes* sp. B. described below.

Stachyodes sp. A
(Fig. 53A,B.)

MATERIAL. JCUF11385-8 from JCUL788.

DESCRIPTION. Skeleton of thin branches, 1.9-3.6mm diameter (mean = 2.3, σ= 0.4, n=15), caniculate, with axial canal 0.3-0.6mm in diameter (mean = 0.4, σ= 0.1, n=15). Microstructure unrecognisable due to poor preservation. One axial canal demonstrates a dissepiment.

MORPHOMETRICS. Data are summarised below and in Figure 54.

Specimen	D mean	Dσ	n	A mean	Aσ	n
JCUF11385	2.4	0.6	5	0.4	0.1	5
JCUF11386	2.4	0.3	4	0.35	0.05	4
JCUF11387	2.4	0.4	3	0.5	0.1	3
JCUF11388	2.2	0.2	3	0.4	0.05	3

REMARKS. The dendroid form and coalesced skeletal elements indicate affinities with *Stachyodes* but poor preservation renders a specific assignment impossible. The branch sizes are small for *Stachyodes*, but within the ranges of some species Cockbain (1984: 29).

Stachyodes sp. B.
(Fig. 53C,D.)

MATERIAL JCUF11402 from JCUL787.

DESCRIPTION. Single specimen, many slender branches 1.1-3.5mm in diameter (mean = 2.8, n=10) most commonly with axial canal 0.3-0.7mm wide (mean =0.4mm, n=9). No dissepiments observed within the axial canal. Pillars and laminae poorly differentiated giving rise to fused skeletal elements. Microstructure fibrous, normal to axial canal and skeletal margin. In transverse section microstructure has melanospheric appearance.

REMARKS. The coalesced skeletal architecture, combined with the fibrosity of the skeletal elements suggest affinities with *Stachyodes*, but the limited material precludes adequate assessment of this morph, which is best left under open nomenclature. *Stachyodes* sp. B has branches of a smaller diameter than *S. costulata* and *S. crassa*, and a more closed skeletal arrangement than the latter. It appears to differ from *Stachyodes* sp. A on the basis of its slightly larger size and the unusual microstructure

COENOSTROMATIDAE
Waagen & Wentzel, 1887

Coenostroma Winchell, 1867
Coenostroma Winchell 1867: 99; Nicholson 1886b: 11; Stock, St. Jean & Otte 1990: 3.; Stearn 1993: 221.

TYPE SPECIES. *Stromatopora monticulifera* Winchell, 1866 (p. 91) , from the Middle Devonian Traverse Group, Michigan, North America, by subsequent designation of Miller 1899.

DISTRIBUTION AND AGE. According to Stearn (1993) the genus is mostly restricted to the Middle Devonian but probably ranges from latest Silurian and throughout the Devonian. Its known geographic distribution is North America, China, Australia and Europe.
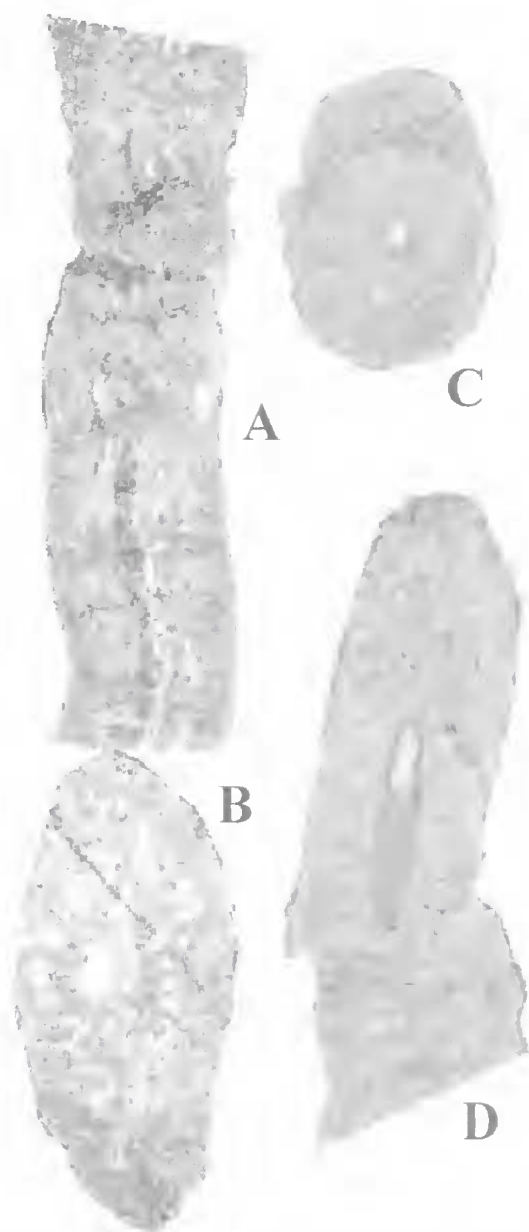
FIG. 53. A,B, *Stachyodes* sp. A. × 10 JCUF11388. A, transverse section; B, longitudinal section. C,D, Stachyodes sp. B. × 10 JCUF11402. C, transverse section; D, longitudinal section.

REMARKS. The genus has been recently resurrected and reviewed by Stearn (1993), who stressed the imperfect grid, long persistent elements and local microlaminae. He discussed the historical placement of the genus within *Stromatopora*, the reasons for its separation, and the characteristics of type material.

Coenostroma burdekinense sp. nov.
(Fig. 55)

ETYMOLOGY. From the Burdekin River.

MATERIAL. Holotype JCUF12763 from JCUL793; paratypes JCUF12764-6, 11788 from JCUL787; JCUF11783 from JCUL794; additional material JCUF12768-12771 from JCUL788.

DIAGNOSIS. *Coenostroma* with a relatively dense skeletal grid network in vertical section, coenosteles spaced approximately 6 per 2mm, thick and somewhat microreticulate. Coenostromes continuous and spaced approximately 5-6 per 2mm, interrupted by pores or locally replaced by microlaminae or dissepiments and composed of one or 2 microlaminae consisting of rows of melanospheres. Tangential section shows a dense, porous network, and small, rounded or irregular galleries.

DESCRIPTION. Skeletal shape low to high domical, up to 12cm wide, growth surfaces moderately to gently undulose. Common, well-spaced syringoporid symbionts are present in many specimens. In vertical section skeletal elements form a dense, moderately regular grid occupying up to 60% of the skeleton, in which coenosteles are a little more prominent than other elements. Coenosteles variable in length, some persist for up to 4 coenostromes and are generally upright, but shorter coenostromes may be oblique, commonly dividing upwards, independent of coenostroms, and consequently highly variable in thickness. Coenosteles composed of melanospheric material with the melanospheres commonly aligned, especially in thicker elements, to form a microreticulate network. Vertical elements variably spaced, 4-9 per 2mm (mean = 6.2, σ= 1.3, n=40) dependant on thickness which ranges from 0.08-035mm (mean = 0.19, σ=0.08, n=40).Horizontal elements long, commonly locally replaced by microlaminae or short dissepiments, commonly interrupted by pores. Coenostromes 4-8 per 2mm (mean = 5.2, σ=1.1, n=35), generally a little thinner than coenosteles 0.08-0.30mm (mean = 0.17, σ=0.06, n=35), commonly composed of one or 2 microlaminae or aligned, fine melanospheres completing a reticular microstructure; but may be melanospheric. Galleries small, rounded or

irregular, with common dissepiments. Uncommon astrorhizae appear as disordered groups of 1-3 subvertical septate tubes, accompanied by up-arching of coenostroms. Tangential section shows a dense skeletal network, with wide bands of dense skeleton pierced by small rounded pores dominating the skeleton. Interlaminar areas dense; galleries small and rounded to irregularly vermiform. Astrorhizae up to 8mm wide and consist of long, unwalled canals which are complexly branched at their distal ends and commonly crossed by dissepiments. Syringoporids are relatively uniformly distributed in tangential section.

FIG. 54. Branch diamcter plotted against axial canal diameter for *Stachyodes* sp. A. from the Burdekin Formation.

MORPHOMETRICS.

Specimen	P2	Pt	L2	Lt
12763	5.1 (0.7)	0.22 (0.08)	5.9 (1.2)	0.16 (0.06)
12765	7.0 (1.5)	0.17 (0.08)	6.0 (1.1) n=5	0.15 (0.06)n=5
12766	6.7 (1.1)	0.19 (0.06)	5.2 (0.6)	0.18 (0.06)
11788	5.8 (0.9)	0.20 (0.06)	5.3 (1.0)	0.18 (0.07)
Average	6.2 (1.3)	0.19 (0.08)	5.5 (1.1)	0.17 (0.06)

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian.

REMARKS. The reticulate microstructure, the grid-like network and the reduced galleries place the taxon within *Coenostroma* Winchell. The type species *C. monticuliferum* (Winchell) has a similar style of skeletal organisation, but has more closely spaced skeletal elements. *C. beachvillense* (Fagerstrom) shows more isolated pillars in interlaminar spaces in tangential section. *C. burdekinense* differs from *C. wyatti* sp. nov. by having shorter coenosteles without clear axes and its somewhat more dense skeletal network in vertical section.

Coenostroma wyatti sp. nov.
(Fig. 56)

MATERIAL. HOLOTYPE: JCUF12040 from JCUL794. PARATYPES: JCUF12037 from JCUL794; JCUF12043-12049 from JCUL787; JCUF12050, 12051 from JCUL778; JCUF12052 from JCUL788; JCUF12053 from JCUL781.
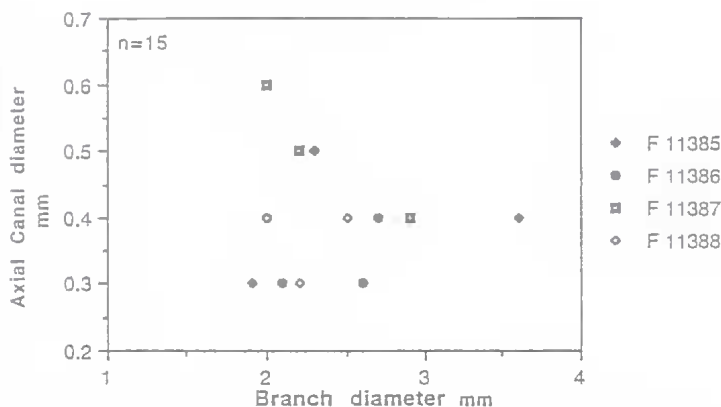
ETYMOLOGY. For Donald Hector Wyatt, formerly of the Geological Survey of Queensland for his voluminous contributions to the geology of the Townsville hinterland.

DIAGNOSIS. *Coenostroma* which in vertical section shows a regular grid formed by long, continuous, clear-centred, peripherally melanospheric coenosteles which are spaced 9-14 per 5mm 0.07 to 0.25mm thick, spool-shaped between horizontal elements, and variable coenostroms; often long but discontinuous; spaced 8-15 per 5mm, and 0.05-0.27mm thick. Dissepiments common in the irregular to rounded galleries. Coenostromes commonly with one, or rarely, 2 microlaminae, mostly melanospheric with rare relict microreticulate structure. In tangential section elements form an irregular to labyrinthinc arrangemcnt, coenosteles vermiform to rounded where isolated with clear centres and coenostromes as arcuate zones with many rounded small pores.

DESCRIPTION. Skeleton medium to high domical, up to 8.5cm high and 9.2cm wide. Horizontal elements moderately arched forming enveloping surfaces, but only moderately undulose. Astrorhizal canals inconspicuous in hand specimen. Syringoporid symbionts abundant in many specimens. In vertical scction the skeleton appears as a moderately regular grid formed by long coenosteles and long but generally discontinuous coenostroms. Vertical elemcnts weakly dominate in some specimens, horizontal elements weakly dominate in others; in general they are equally developed.
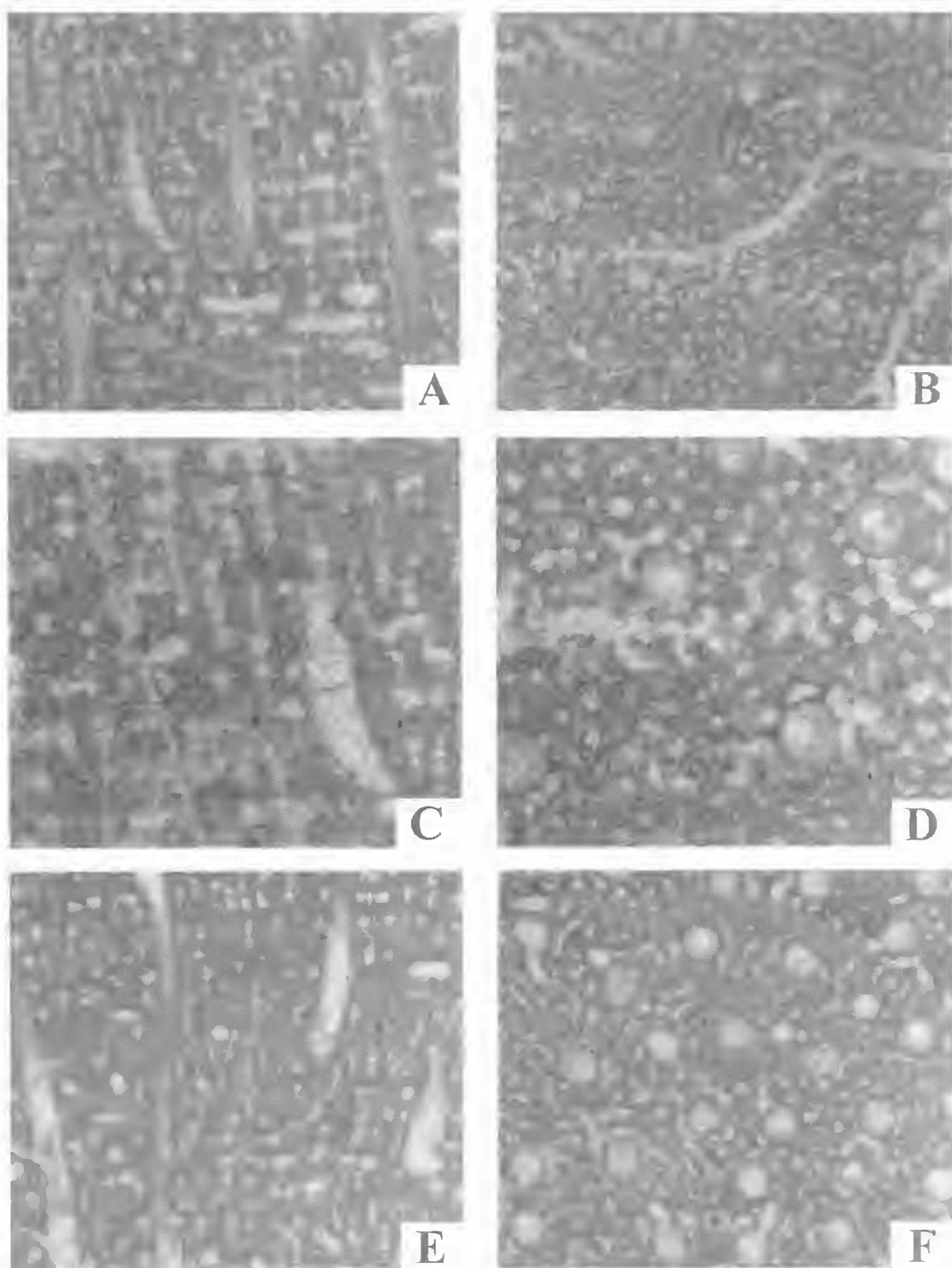
FIG. 55. *Coenostroma burdekinense* sp. nov. A-D, Holotype JCUF12763. A, vertical section × 10; B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, paratype JCUF11783. E, vertical section × 10; F, tangential section × 10.
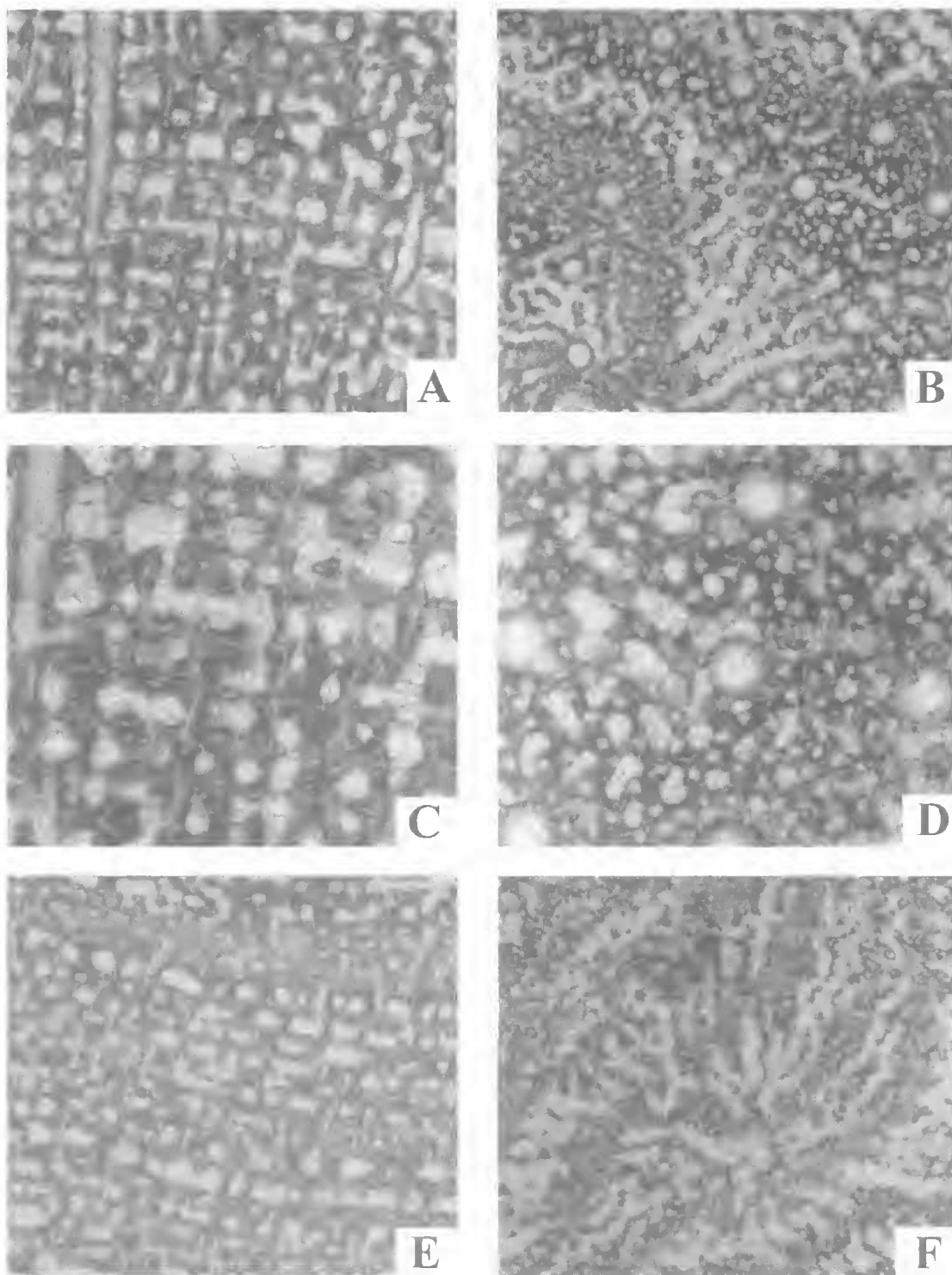
FIG. 56. *Coenostroma wyatti* sp. nov. A-D, Holotype JCUF12040. A, vertical section × 10. B, tangential section × 10; C, vertical section × 20; D, tangential section × 20. E, F, Paratype JCUF12042. E, vertical section × 10; F, tangential section × 10.

Coenosteles long, persistent for up to 16 coenostromal thicknesses, and are somewhat spool shaped in intercoenostromal space. They are 0.07-0.25mm (mean =0.16) thick, and are spaced 9-14 per 5mm (see below), with a clear axis comprising approximately half their width, with a finely melanospheric periphery. Coenostromes are of 2 types. Long discontinuous coenostromes dominate the skeletal grid, 8-15 per 5mm, 0.05-0.27mm thick. They commonly have a thin, compact, dark line, or, more rarely, 2 dark lines, which are interpreted as microlaminae. Shorter horizontal elements are irregular, sporadically oblique, with common bulbous projections on both upper and lower surfaces. They are uncommonly oblique. The coenostromes are dominantly melanospheric, but the texture varies from very fine dark spots to one or 2 larger dark spots. In places, the finer-grained melanospheres are aligned suggesting a relict, if weak, reticulate microstructure. Galleries in vertical section are rounded, or commonly irregular, vertically or horizontally elongate, sporadically forming short coenotubes. They are commonly crossed by thin, gently upwardly arcuate dissepiments. The skeletal elements are modified adjacent to syringoporid corallites; coenostromes continue unflexed to a thin (0.05-0.12mm) peripheral sheath of melanospheric skeletal material. In tangential section intersections of coenostromes form wide arcuate zones of dense skeleton. Within these zones the skeletal material is melanospheric, and abundant circular pores pierce the coenostroms. Intercoenostromal spaces are marked by pillar intersections which are short to long vermiform, less commonly rounded, with the former sporadically forming a local labyrinthine network. Pillars are commonly, especially where isolated, conspicuously clear-centred. Galleries are irregular to labyrinthine but few dissepiments are visible in tangential section. Intersections of syringoporids are surrounded by a totally enveloping sheath of skeletal material.

MORPHOMETRICS.

Specimen	P5	Pt	L5	Lt
JCUF12038	11.7 (1.3)	0.17(0.05)	11.6 (1.0)	0.19 (0.11)
JCUF12040	11.2 (1.2)	0.19 (0.04)	11.2 (1.4)	0.19 (0.04)
JCUF12041	12.3 (1.1)	0.15 (0.03)	10.8 (1.4)	0.16 (0.07)
JCUF12042	11.6 (1.1)	0.13 (0.04)	12.7 (1.4)	0.15 (0.07)
Average	11.7 (1.3)	0.16 (0.04)	11.6 (1.5)	0.17 (0.08)

DISTRIBUTION AND AGE. Burdekin Subprovince, north Queensland, Middle Devonian, Givetian.

REMARKS. Assignment to *Coenostroma* is justified on the basis of the regular, if imperfect, grid in vertical section, local microlaminae and relict, but vague, microreticulate microstructure. Problems with this assignment are the fine melanospheric nature of the majority of skeletal material. The taxon is distinguished by the clear centred pillars, a feature lacking in the type species. This attribute, coupled with the melanospheric dominated-microstructure may warrant erection of a new genus. The taxon, however, can be comfortably accommodated within the generic concept of *Coenostroma* advocated by Stearn (1993) and erection of a new genus on the basis of one partially problematic taxon is not warranted.

Illustrations of the type species by Galloway & Ehlers (1960) and Stearn (1993) are broadly comparable but *C. wyatti* shows a much more regular network. *Coenostroma beachvillense* (Fagerstrom) resembles this new taxon but its horizontal elements are more prominent. *Coenostroma* sp. described by Webby, Stearn & Zhen (1993) from the Lower Devonian of Victoria also grossly resembles *C. wyatti*, but has fewer pores, no clear centred pillars, more common dissepiments and its laminae are a little more prominent.

Stearn (pers. comm.) has suggested close comparison with *Psuedotrupetostroma* Khalfina & Yavorsky, 1971. Whilst this is an attractive accomodation for this material, the relict reticultion of the microstructure is in contrast to the generic revision given by Stearn (1993). Webby (pers. comm.) and Stock (pers. comm.) have suggested the material may be accomodated within *Parallelopora*, but that genus is characterised by coarse reticulated microstructure, not the fine structure found within this taxon.

Parallelopora Bargatzky, 1881a.

TYPE SPECIES. *Parallelopora ostiolata* Bargatzky, 1881a, by subsequent designation from the Middle Devonian of Paffrath, Germany.

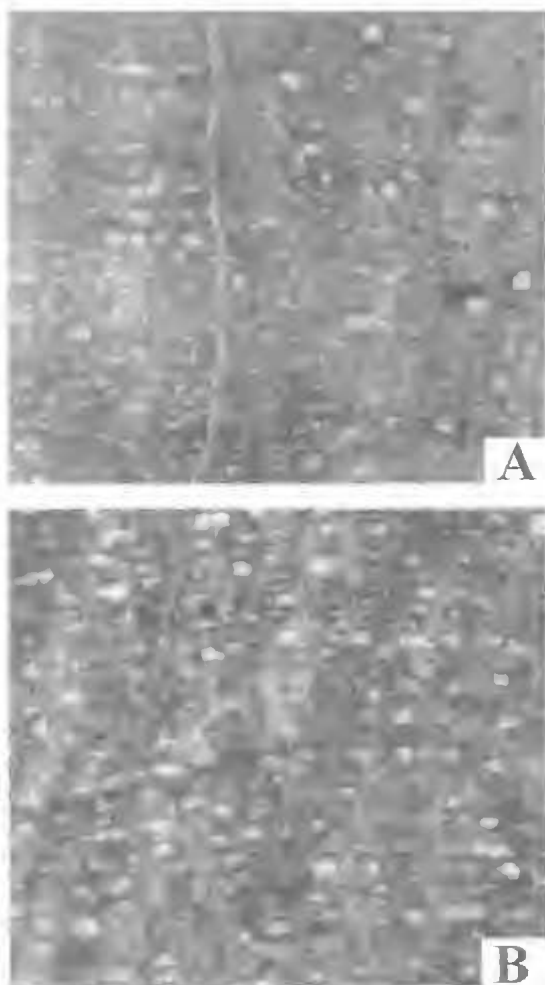REMARKS. See Stearn (1993) for a synonymy, diagnosis and recent review.

FIG. 57. *Parallelostroma* sp. JCUF12759 A,
vertical section x 10. B, tangential section ⨯ 10.

?Parallelopora sp.
(Fig. 56)

MATERIAL. JCUF12759-62 all from Burdekin Downs,
JCUL781.

DESCRIPTION. Skeleton laminar to very low
domical, up to 2cm thick, fragmental so that
maximum width is indeterminate. In vertical
section a fine, irregular grid is formed by long,
impersistent coenostromes and thick, moderately
continuous coenosteles. Coenosteles are medium
to long, continuous through up to 7 coenostroms,
spaced at 6-9 per 2mm. They are 0.05-0.22mm
thick, generally thicker than coenostroms.

Coenosteles are clearly microreticulate,
consisting of generally 2, but up to 4, rows of
aligned melanospheres which commonly
coalesce into micropillars. Coenostromes are
continuous but impersistent, commonly replaced
by microlaminae. They are spaced at 7-9 per
2mm, and they are generally thinner than vertical
elements (0.05-0.12mm). They consist of one or
2 continuous lines of specks which very
commonly form microlaminae, and combine
with vertical microstructure to produce a
reticulation. Galleries are very small and
rounded, or vertically elongate. They are crossed
by numerous dissepiments.

There are a few thin vertical or oblique tubes,
interpreted as intergrowths of an indeterminate
organism. In tangential section material is poorly
preserved. Elements form a closed network with
small rounded galleries/ coenotubes.

REMARKS. The characteristic microstructure,
and the reduction of galleries in tangential
section suggests affinity with *Parallelopora*,
based on the revised diagnosis of Stearn (1993).
The relative continuity of the horizontal
elements, however, is in disagreement with this
assignment and the specimen could as easily be
placed within *Parallelostroma*. Coenosteles are
dominant, but the horizontal elements are
certainly not suppressed. The generic assignment
is questionable.

ACKNOWLEDGEMENTS

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Ravenswood Granodionte   Burdekin Formation
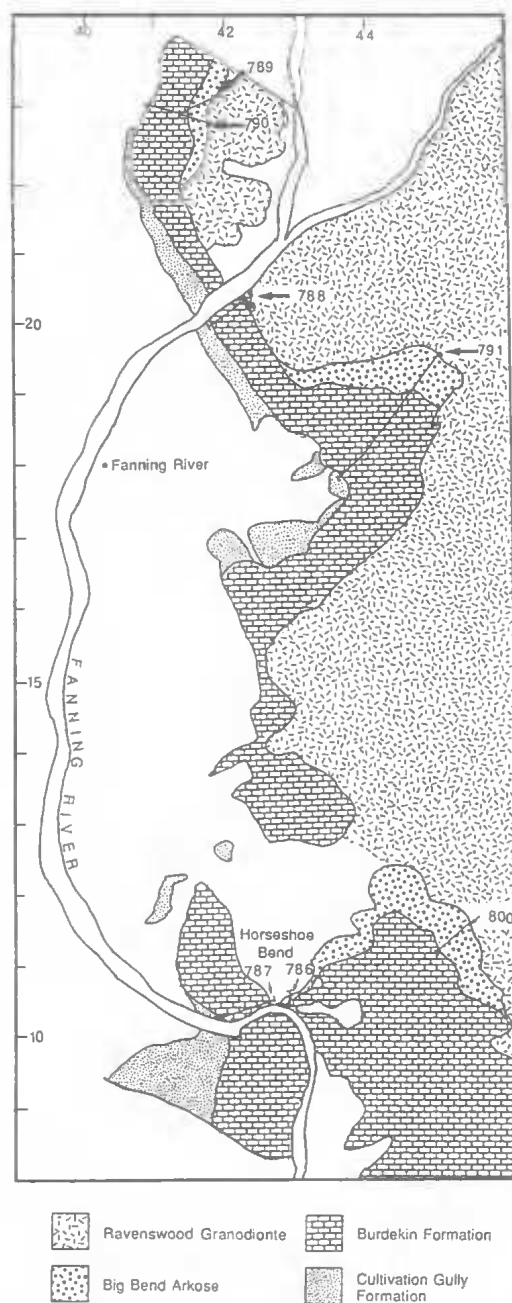
Big Bend Arkose   Cultivation Gully Formation

FIG. 58. (Appendix). Localities in the Fanning River area.

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APPENDIX 1
List of Localities (see Figs. 58,59)

|	
JCUL778	Fletcherview station, east side of Burdekin River, downstream from 'Little Rocks'. Section from base of Fanning River Group to approximately 45m up sequence. DU155027 to DU157029.
JCUL779	Fletcherview Station, north bank of Burdekin River upstream from "Little Rocks". Section from DU149025 to DU144027.
JCUL780	Fletcherview Station, west bank of Burdekin River, downstream from Little Rocks. Section from lower Burdekin Formation, upwards (NE) 40m. DU153030 to DU157031, JCUL781 Burdekin Downs Station, North Bank of Burdekin River downstream from confluence of Arthurs Creek. Section from lower Burdekin Formation at DU171032 to top of prominent cliffs at DU169035.
JCUL781	Fletcherview Station, west bank of Burdekin River, downstream from Little Rocks. Section from lower Burdekin Formation, upwards (NE) 40m. DU153030 to DU157031.
JCUL782	Western equivalent of main framestone unit in JCUL781 at DU167036, downstream from confluence of Arthurs Creek, Burdekin River, Burdekin Downs Station
JCUL783	Small un-named tributary of Arthurs Creek, joining at western side of Arthurs Creek near confluence with Burdekin River at DU165040. Burdekin Downs Station Creek bank section of Big Bend Arkose.
JCUL784	North bank of Burdekin River, Burdekin Downs Station, approximately 2km upstream from homestead. A short section through the Big Bend Arkose- Burdekin Formation transition at DU180024.
JCUL785	Hill directly behind Burdekin Downs Station homestead, at DU200 012. (Small bivalve collection from Burdekin Formation).
JCUL786	Tributary of Fanning River at Horseshoe Bend west of Horseshoe Bend Mill, Fanning River Station. Short section from unconformity to lower Burdekin Formation at DU428105
JCUL787	North Bank of Fanning River at Horseshoe Bend, section along River running east to west from DU425105 to 418103 along river flat.
JCUL788	Fanning River Type Section, Fanning River, Upstream from Fanning River Station from DU422204 to DU417202
JCUL789	Fanning River North Section, approximately 3km N of Fanning River type section, in gullies from DU419232 through forest clearing at DU413230 to DU410230. Big Bend Arkose to uppermost Burdekin Formation.
JCUL790	Section in gully approximately 3km N of Fanning River Type section, through Big Bend Arkose and lowermost Burdekin Fmn. From DU417228 to DU414229.
JCUL791	Section across main limestone hills SE of Fanning River type section, comprising all of the Burdekin Formation at its thickest mapped point. DU448194 to DU433178.
JCUL792	Big Bend, Burdekin River, Burdekin Formation only from DU093055 to DU091052.
JCUL793	Outcrop in un-named creek from base of Fanning River Group at DU185 026 upstream for approx 100 metres. Burdekin Downs Station.
JCUL794	Isolated rubblecrop containing abundant well preserved stromatoporoids, N of JCUL781 at DU176037 Burdekin Downs Station.
JCUL795	Rubblecrop along fenceline, on hill 2km N of Burdekin Downs Homestead at DU205 029.
JCUL796	Kirkland Downs, immediately S of road into property at 993604 (Hillgrove 1:100 000).
JCUL797	Turkey Hill, Kirkland Downs Station, 2km to the West of station residence at 979621 (Ewan).
JCUL798	Paynes Lagoon Station, 200m south of Boundary Creek, approximately 800m to the west of cattle yards at 045 467 (Rollingstone).
JCUL799	Paynes Lagoon Station, 400m E of Boundary Mill in Boundary Creek 062 470 (Rollingstone).
JCUL800	In Hills 1km NNW of Golden Valley. Section through Big Bend arkose from DU451115 to 448113.
JCUL801	Mount Podge, Laroona Station, Section from northern edge of rhyolite intrusion to top of Mount Podge Limestone along Running Creek. Laroona Formation and Mount Podge Limestone from 915 639 to 913 649 (Ewan).
JCUL802	Mount Podge Eastern section. Approximately 600m E of Running Creek Section from basal sandstones East of un-named gully N to same Gully, offset 200m E in gully and thence N to base of Keelbottom Group at foot of hill from 920 639 to 920 641 and 922 641 to 921 647 (Ewan).
JCUL803	Fanning River Caves, Rope Ladder Cave, 18m section of Burdekin Formation, through 3 main chambers. 3km SE of Fanning River Station.; part of JCUL791 section DU452 182.
JCUL804	Short section, SW side of Burdekin River at Fletcherview Station, almost opposite JCUL782 with resepect to river DU163 035.
JCUL805	Arthurs Creek, small section thorugh basal units at DU169048.
JCUL806	Mount Podge West section through Limestone approx 2km west of Running Creek, south of main peak at Mount Podge from 892 644 to 895 648 (Ewan).
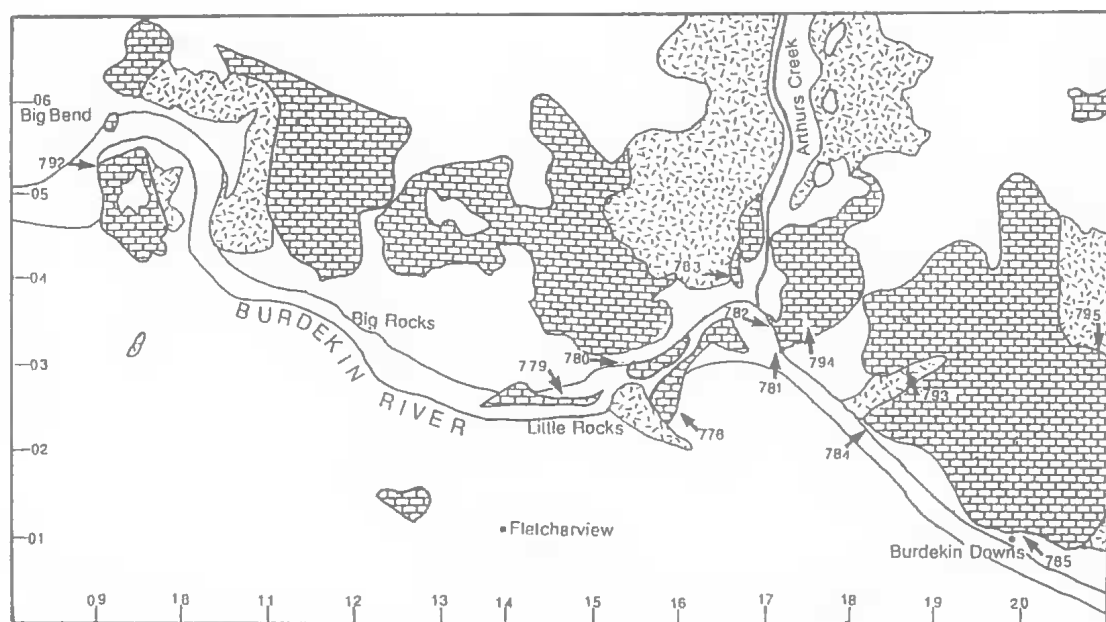
FIG. 59. (Appendix). Localities in the Burdekin Downs-Fletcherview area.